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The roles of community diversity and contact rates on pathogen prevalence

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The complexity of a community can play a fundamental role in the prevalence of pathogens by altering interactions among hosts and pathogen transmission. Information on the frequency of contacts between individuals and the distribution of contact rates in a population is critical to predicting pathogen prevalence. However, contact rates are notoriously difficult to document especially in small, nocturnal species. We have been documenting the contact rates of deer mice (*Peromyscus maniculatus*) in nature with respect to infection with Sin Nombre virus (SNV), a zoonotic pathogen, and the biodiversity of the mammalian community. Our long-term field studies, as well as those of others, revealed that prevalence of SNV in deer mice is related to the complexity of the mammalian community such that pathogen prevalence is lower in more diverse communities. Using a combination of techniques, we found evidence that contact rates between deer mice differ with respect to biodiversity. Deer mice in more complex communities had fewer intraspecific interactions than those in less diverse communities. Contact rates of individual deer mice were highly variable with a minority of the deer mice accounting for a majority of the interactions. Infection with SNV was related to risk-taking behavior; animals categorized as "bold" were 3 times more likely to be infected than "shy" deer mice. Results of these studies have implications for pathogen management in wildlife and humans.

Key words: contact rates, density, *Peromyscus*, Sin Nombre virus, species diversity

The biodiversity of an ecosystem influences many community-level functions such as productivity, resistance to invasion, and stability (Naeem and Shibin 1997; Tilman et al. 1997; Knops et al. 1999; Smith and Knapp 1999). More recently, species diversity has been identified as an important factor in regulating the dynamics of pathogens (Keesing et al. 2010). The way in which biodiversity alters pathogen prevalence is contingent in part upon whether diversity increases or decreases contact between potential hosts. These divergent outcomes of the impact of species diversity on pathogen prevalence are described within a framework of 2 hypotheses known as the "dilution effect" and "amplification effect" or "rescue effect" (Ostfeld and Keesing 2000; Gilbert et al. 2001; Keesing et al. 2006). The dilution effect predicts that species diversity decreases pathogen prevalence through mechanisms such as decreased host density, reduced encounters between hosts, or reduced host survival (Ostfeld and Keesing 2000; Gilbert et al. 2001; Keesing et al. 2006). In contrast, the amplification effect predicts increased pathogen prevalence with greater species diversity, through increased encounters between hosts (Keesing et al. 2006), through interactions between primary and secondary hosts, or by maintenance of the pathogen by secondary hosts even when primary hosts are at low densities (LoGiudice et al. 2003; Keesing et al. 2006). Over the past several years, the importance of species diversity on pathogens has been documented in a wide variety of host–pathogen systems (Keesing et al. 2010).

Knowledge of contact rates between members of the community is a key component in predicting whether species diversity will increase or decrease pathogen prevalence. Contact rates are a central variable in conventional epidemiological models, as they are typically a component of β, the transmission coefficient (Anderson et al. 1986). Despite their significance in predicting pathogen transmission, contact rates are rarely measured because of the inherent difficulties associated with observing sufficient numbers of interactions between individuals in nature (Ramsey et al. 2002; Prange et al. 2006). Contact rates between large mammals can be obtained by outfitting individuals with collars that provide data on an animal's position (Jolles and Ezenwa 2015; Schauber et al. 2015). This approach is not suitable for small, solitary mammals such as

rodents and bats, yet these species host a large number of zoonotic agents (Luis et al. 2013).

Since 2002, our research group has focused on understanding the role of species diversity and the mechanisms by which it acts on pathogen dynamics in natural host populations. Our study system consists of deer mice (*Peromyscus maniculatus*), a generalist species common in many nocturnal rodent communities, and Sin Nombre virus (SNV), a zoonotic pathogen of significant public health concern in the western United States of America. We have been investigating how biodiversity of the community influences encounter rates of deer mice and the consequences for pathogen prevalence. For directly transmitted pathogens such as SNV, contacts between infected and susceptible individuals represent the underlying mechanism through which diversity is expected to act. Both the dilution and amplification hypotheses predict that species diversity will change the rate of contact between individuals, and other studies have shown that diversity may also change the frequency and the nature of contacts among conspecifics (Ovadia et al. 2005). However, contact rates are not easily obtained for small, solitary, nocturnal mammals such as deer mice. While radiotelemetry may seem an obvious technology, the weight of the transmitters and the presence of observers can alter the behavior of rodents. Additionally, telemetry location estimates are usually too large (within meters) to define probable contacts between animals with small home ranges, like rodents, and the costs prohibit marking an entire rodent community. These limitations may suggest that deer mice are not a good model system in which to study pathogen transmission (Jolles and Ezenwa 2015). To overcome these constraints in our system, we used one conventional method (with modifications) and developed a new method that makes estimating contact rates possible on a large scale in this study system.

Here, we review some of the highlights from more than a decade of work on deer mouse dynamics at population and community levels. We first present a short background section on the host–pathogen system followed by methods we have used. We then present our results and discuss our findings regarding the influence of biodiversity and contact rates on pathogen prevalence in populations of deer mice. We conclude by presenting some of the upcoming technologies that will further enhance our ability to study contact rates of animals.

Natural history of the host and pathogen.—Sin Nombre virus is one of more than 40 species in the genus *Hantavirus*, family Bunyaviridae. On a global scale, hantavirus infections in humans result in > 200,000 hospitalizations annually (Bi et al. 2008). Unlike the other genera in Bunyaviridae, hantaviruses are not thought to be transmitted by arthropod vectors but rather are directly transmitted from mammal to mammal. All hantaviruses have a primary mammalian host (mostly rodents) with which they have had a long coevolutionary history (Abbott et al. 1999; Yates et al. 2002). The primary host for SNV is the deer mouse, *P. maniculatus* (Childs et al. 1994), although other closely related mammalian species (i.e., *Peromyscus truei* and *Neotoma lepida*) are putative reservoirs (Dearing et al. 1998). Transmission between rodents is thought to occur through exchange of infected saliva during aggressive encounters (Calisher et al. 2007; Douglass et al. 2007). However, other routes (exposure to excreta from an infected animal, grooming, and arthropod bites) have been proposed but have not been thoroughly investigated (Mills et al. 1997; Calisher et al. 1999; Pearce Duvet et al. 2006).

In the natural host, SNV establishes a lifelong, seemingly asymptomatic infection (Botten et al. 2003). During the acute phase of infection (≤ 45 days postinfection), virus is found in the vascular endothelium of most host tissues (Botten et al. 2000, 2003). However, during the persistent phase of infection (≥ 60 days postinfection), 2 distinct phenotypes of infection (*restricted* or *disseminated*) are observed (Botten et al. 2000, 2003). Mice with the restricted pattern exhibit viral antigen expression in the heart, brown adipose tissue, and/or lung with no evidence of active viral replication in these tissues and an absence of virus in the blood. In this phase, the virus appears to be in a period of replicative quiescence whereby only viral antigen and genomic viral RNA are maintained (Botten et al. 2000, 2003). In contrast, animals with the disseminated pattern have viral antigen expression in more than 5 tissues; replicative RNA in the heart, lung, and brown adipose tissue; and detectable levels of virus in the blood (Botten et al. 2000, 2003). While heart, lung, and brown adipose tissues are critical depots for the virus, it remains unknown what factors (viral and/or host) regulate viral replication to an active or quiescent state during persistent infection (Botten et al. 2000, 2003). It seems likely that transmission is more likely to occur during the disseminated phase although this hypothesis requires further examination (Botten et al. 2000, 2003).

The relationship of hantaviruses and their rodent hosts is an ancient one with a coevolutionary history spanning millions of years (Yates et al. 2002). As is the case for other hosts of hantaviruses (Gavrilovskaya et al. 1990; Bernshtein et al. 1999; Kallio et al. 2006, 2007), deer mice infected with SNV appear asymptomatic (O'Connor et al. 1997; Botten et al. 2000, 2003) although histopathological changes have been observed (Netski et al. 1999; Lehmer et al. 2010; McLean et al. 2012). Some have suggested that the depressed immune response observed in infected deer mice represents a mutually coadaptive evolutionary event that permits the persistence of the virus (Schountz et al. 2007). In contrast, several other studies have demonstrated that SNV may negatively impact the fitness of deer mice living under natural conditions, as seropositive deer mice gain less mass compared to uninfected deer mice (Douglass et al. 2007) and have lower survival rates (Douglass et al. 2001; Adler et al. 2008).

Materials and Methods

To understand the role of species diversity on SNV prevalence, we studied rodent communities located within the juniper-sagebrush habitat of the Great Basin desert in Utah. These communities represent good wild systems for such studies for 2 reasons (Jolles and Ezenwa 2015). First, SNV prevalence

(0–50%) spans the range seen across all habitat types (Otteson et al. 1996; Boone et al. 1998; Mills et al. 1998; Kuenzi et al. 1999; Douglass et al. 2001; Mackelprang et al. 2001). In addition, rodent species diversity also varies considerably between sites within the same habitat type (Brown 1973; Clay et al. 2009c). Low-diversity communities consist of deer mice only or 1 additional species, whereas the most diverse communities have 7 nocturnal rodent species of varying abundance. Secondary reservoirs such as pinyon mice (*P. truei*) and desert woodrats (*N. lepida*) co-occur with deer mice and may serve to amplify or maintain SNV in the local community, even when deer mouse density is low (Clay et al. 2009c). However, the competence of these secondary reservoirs is currently unknown and is difficult to test because it is now required that researchers use a Biosafety Level 4 facility to work with animals infected with SNV and because of the difficulty of infecting rodents with SNV under laboratory conditions (Centers for Disease Control and Prevention 1994; Botten et al. 2002). Conversely, heteromyid rodents such as Ord's kangaroo rat (*Dipodomys ordii*) and western pocket mouse (*Perognathus parvus*) also co-occur with deer mice in the Great Basin; these rodents are not SNV reservoirs and can achieve relatively high population densities. Heteromyids are frequently present in high diversity communities and may "dilute" or reduce SNV prevalence.

In our studies, rodent communities were sampled from a maximum of 16 sites each 3.1 ha in size and at least 700 m apart in the West Tintic Mountains of central Utah (Juab and Utah Counties). Big sagebrush (*Artemisia tridentata*) and Utah juniper (*Juniperus osteosperma*) were the dominant plant species; however, we selected sites that varied in shrub cover and bare ground, as both have been linked to diversity in rodent community composition (Cui et al. 2005; Valone and Sauter 2005; Alain et al. 2006). For more detail on the study sites, see Lehmer et al. (2008). Rodent sampling occurred once per site in spring and autumn from 2002 through 2011. We could not sample all 16 sites simultaneously; the spring sampling occurred in May and June, whereas the autumn samples were collected in late August, September, and October. Sites were trapped for 3 consecutive nights per season (spring and autumn). At each site, we livetrapped rodents using 148 traps (H.B. Sherman Traps, Inc., Tallahassee, Florida) distributed in a "web" configuration following the methods of Mills et al. (1999). Upon capture, we identified animals to species, and sex and weight were recorded. We marked all individuals with uniquely numbered ear tags.

To determine SNV status of *P. maniculatus*, we collected approximately 0.2 ml of blood at the time of initial capture for each trapping season and tested for SNV antibodies (Clay et al. 2009c). All techniques for capturing and handling animals were approved by the Institutional Animal Care and Use Committee of the University of Utah and conformed to the guidelines for use of wild mammals in research outlined in Sikes et al. (2011).

To estimate contact rates in our study, we powder marked 5 randomly selected male deer mice at 12 sites for 2 nights in the spring and autumn sampling periods over a 2-year period (Clay et al. 2009b). Deer mice were selected on the first morning after processing and maintained in traps with food and bedding until 1–2 h before sunset. Immediately prior to their release, the mice were marked with a fluorescent powder by applying a unique powder color to each mouse (Radiant Color Co., Richmond, California) using a stiff toothbrush. The following morning, all captured deer mice were examined for powder; if present, color and location on the body were recorded for each deer mouse.

In addition, we developed a unique approach to estimating contacts in deer mice using radiofrequency identification technology and foraging arenas (Clay et al. 2009a). We approximated contacts between deer mice and other rodents at 5 of the study sites by using foraging arenas equipped with passive integrated transponder (PIT) antennae and data loggers (FS2001FT-ISO; Biomark, Inc., Boise, Idaho). Time constraints and equipment limitations meant that sites were sampled consecutively, not simultaneously, over the course of 1 month. Prior to estimating contact rates, the 5 sites were trapped as described above. We injected subcutaneously a PIT tag between the scapulae of all rodents trapped. PIT tags uniquely mark each animal and send a signal that is read by a PIT antenna. Within 1 week after mark-recapture sampling, 12 foraging arenas were placed at a site for 3 nights. Arenas were placed throughout the site in locations where deer mice had been captured during the mark-recapture study. At sunset each night, foraging arenas (30-cm diameter) were filled with 2 liters of sand plus 6 g of millet to attract rodents. Antennae were placed below the arenas with data loggers to continuously record the identity and time spent in the foraging area for any tagged individual on or within 0.5 m of a tray. After recording rodent visits for 3 consecutive nights, data from loggers were downloaded onto a laptop computer. From these data, we determined which individuals visited arenas. Apparent contacts between individuals were defined as the presence of 2 individuals at a foraging arena within 15 s of one another. This length of time was appropriate given the 5-s lag in the readers coupled with our video analysis of deer mice at the foraging arenas (described below). We also determined the duration of each apparent contact at each arena.

Our research using PIT tag readers and foraging arenas was largely inferential in that we assumed contact at foraging arenas when 2 rodents were on the trays within 15 s of one another. However, it was possible that rodents were within range of the tag reader at the same time but not in direct contact with one another. Additionally, the nature of the contact (aggressive or nonaggressive) was unknown. Given that SNV is thought to be transmitted through aggressive encounters (Calisher et al. 2007; Douglass et al. 2007), determining whether there is physical contact between animals and the nature of the contact is crucial. Therefore, we added infrared cameras to our system; cameras allowed us to directly study the behavior of these small, quick, nocturnal rodents without the interference of human observers. We conducted a study where we trapped rodents at 2 sites for 3 nights prior to camera observation (Dizney and Dearing 2013). Each rodent was injected with a PIT tag before release. Camera observation occurred for 4 consecutive nights immediately after the 3 nights of trapping in May, July, and September over a 3-year period (2009–2011). We placed 9 foraging arenas with

PIT antenna and data loggers (as described above) 20 m apart in a 3×3 grid within the same area where trapping occurred. Additionally, a video camera was mounted on a metal pole approximately 1 m above the foraging tray and directed at it. All 9 cameras were attached to a centrally located computer by above ground wires. The computer captured and stored video imagery at a rate of 4 frames/s. Observation ceased at sunrise. Software from TimeScience integrated the video and PIT antennae data, such that the identity, demographic data, and infection status of all marked rodents on the trays were known (Brown 2009). We documented the frequency of interactions and the nature of the interactions. We categorized deer mice as "bold" or "shy" based on their behaviors and compared behaviors of infected and uninfected deer mice (Dizney and Dearing 2013).

Results

Our studies of the rodent community in the Great Basin desert revealed that species diversity was negatively correlated with SNV prevalence in deer mice, following the predictions of the dilution effect (Clay et al. 2009c). Surprisingly, host density did not appear to play an important role in this directly transmitted virus (Clay et al. 2009c). Although deer mouse density was lower at sites with higher species diversity, there was not a significant relationship between density and prevalence (Clay et al. 2009c; Fig. 1). Deer mouse persistence, which we defined as the length of time an individual was present on the site (determined by recapture), was significantly lower on the higher diversity sites, which suggests that the longevity of a host in an area or its persistence on a site may be an important factor regulating SNV prevalence (Clay et al. 2009c). Increased turnover of animals on higher diversity sites could reduce territoriality and also decrease interactions that result in the transmission of SNV between deer mice.

Using both techniques (powder marking and PIT technology), we found that deer mice varied significantly in the number of encounters that they had with other deer mice (Clay et al. 2009b). The vast majority of marked deer mice (~75% regardless of method) had no interactions with other marked deer mice during multiple days of observation. In addition, the frequency distribution of unique contacts per individual deer mouse was nonnormal but was skewed to the right—highly aggregated, indicating that a small number of deer mice in the population were responsible for a large proportion of the contacts (Clay et al. 2009b). Both marking methods revealed that a minority of the marked individuals (18–25%) accounted for the majority of the encounters (> 76%). Larger-bodied individuals appear to be the functional group with the greatest SNV transmission potential, as they were the ones with the most contacts (Clay 2009b).

Out of 3,000 h of video recording, deer mice were observed for approximately 166 h (5% of total time observed—Dizney and Dearing 2013). Deer mice spent most of their time, at least while foraging, alone. Deer mice were rarely observed in pairs at the trays (1.25 h or 0.04% of the total observation time). During these observations, 25% of the interaction time was spent with 1 deer mouse actively "avoiding" another deer mouse (Fig. 2). We described avoiding as a deer mouse leaving the camera's view when in the presence of another deer mouse, or a deer mouse entering a foraging tray within 10 s of another deer mouse leaving the tray, presumably waiting outside the camera's view until the occupant of the tray left. We observed 4 behaviors where deer mice engaged in interactions with one another, 2 of which were aggressive and 2 nonaggressive. The 2 aggressive behaviors were chasing (1 deer mouse in pursuit of another without any contact) and fighting (aggressive contact). The 2 nonaggressive behaviors were sharing (2 deer mice feeding on the tray at the same time) and grooming (any

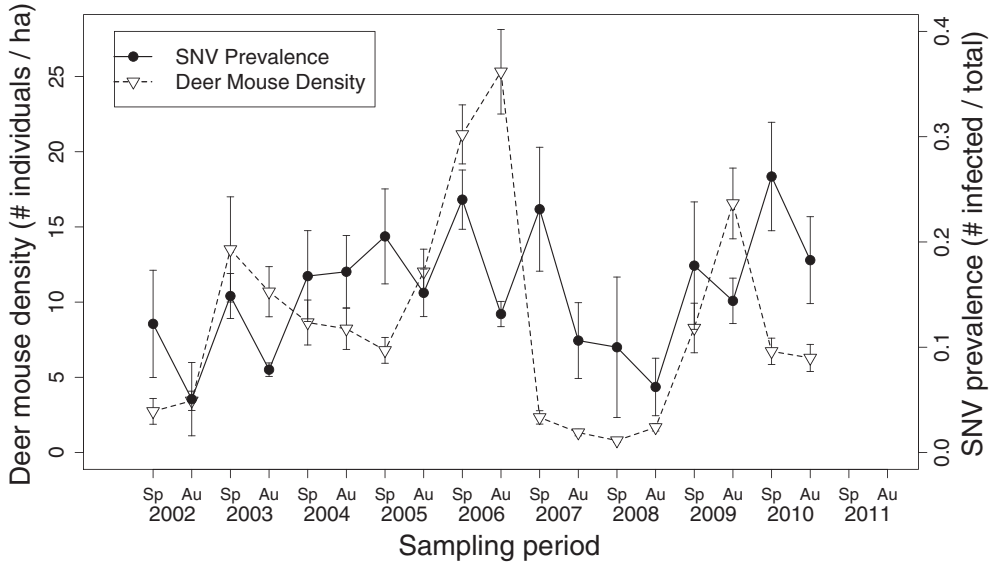

Fig. 1.—Mean density of deer mice (*Peromyscus maniculatus*; triangles) and mean prevalence of Sin Nombre virus in deer mouse populations in the Great Basin Desert, Utah. The number of study sites sampled at a time varied from 6 to 16. Sites were sampled in spring (Sp) and autumn (Au). The relationship between density and prevalence was not statistically significant ($r^2 = 0.06$; $P = 0.33$).

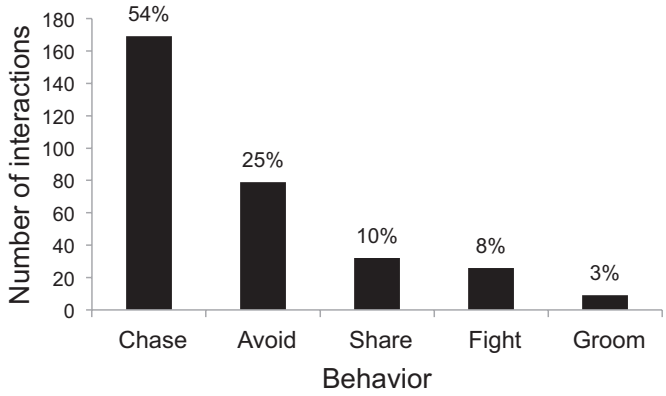

Fig. 2.—Types, number, and percentages of behavioral interactions of deer mice (*Peromyscus maniculatus*) observed on foraging arenas in the Great Basin Desert of central Utah. Interactions at foraging arenas were measured using passive integrated transponder technology and infrared cameras. Observation occurred on 2 study sites for 4 consecutive nights in May, July, and September over a 3-year period (2009–2011).

nonaggressive behavior between 2 deer mice such as cleaning or nuzzling). The aggressive behaviors of fighting and chasing made up the majority of the total interaction time (Fig. 2). The nonaggressive behaviors comprised only a small fraction of the interaction time. We found that SNV-positive deer mice more often engaged in behaviors that increased the likelihood of intraspecific encounters and were more aggressive. Five behaviors that we considered to increase the risk of SNV transmission were used in a principal component analysis to categorize individual deer mice as either "bold" or "shy." The 5 behaviors included time spent on the trays, number of trays visited, number of nights seen on the trays, approximate distance traveled during an observation period, and number of aggressive interactions. "Bold" deer mice were 3 times more likely to be SNV positive than were "shy" deer mice (Dizney and Dearing 2013).

Discussion

Community diversity is an important driver of SNV dynamics in deer mice. High species diversity "diluted" the prevalence of SNV in deer mouse populations. The dilution effect appears to be a common phenomenon in other hantavirus–host systems. At least 7 other studies have documented greater hantavirus prevalence in rodent communities with reduced diversity (Suzán et al. 2008; Tersago et al. 2008; Dizney and Ruedas 2009; Suzán et al. 2009; Carver et al. 2011; Voutilainen et al. 2012). Three of these studies examined SNV dynamics in the United States, 2 examined Chaclo and Calabazo hantaviruses in Panama, and 2 investigated Puumala virus in Europe. Five of these studies were comparisons of habitats with different levels of biodiversity, whereas 2 were manipulative experiments within natural habitats. The effect of diversity on prevalence appears to be the result of more than simply a reduction in host density, as density alone was not predictive of prevalence in 3 of 5 studies that addressed this issue. Taken together, these studies suggest that the dilution effect has broad applicability within the realm of hantavirus prevalence, reaching across types of ecosystems, host, and pathogens, and modes of transmission.

We found that community diversity influenced intraspecific interactions between deer mice (Clay et al. 2009a). Encounters (contact rates) between conspecifics were inversely related to changes in biodiversity as the number of unique encounters and the total number of intraspecific deer mouse encounters were lower at sites with greater diversity (Clay et al. 2009a). However, our results also reveal that diversity did not alter the duration of intraspecific deer mouse contacts, which lasted up to 48 s regardless of community complexity (Clay et al. 2009a).

Prevalence of SNV was related to contact rates between deer mice, as SNV was lower at sites with a lower proportion of intraspecific encounters between deer mice (Clay et al. 2009a). This pattern is consistent with the predictions of the dilution effect hypothesis, as species diversity has the potential to reduce pathogen prevalence in natural populations by reducing encounters between hosts (Keesing et al. 2006). In less complex communities, deer mice encounter one another often, thereby increasing the opportunity for transmission of SNV between individuals (Clay et al. 2009a). This work documented that deer mice have about half as many encounters with conspecifics in high diversity communities and that these conditions also resulted in deer mice having a larger number of interspecific encounters, primarily with individuals that do not host SNV (Clay et al. 2009a).

Physical contacts likely play an integral role in transmission of directly transmitted pathogens, and the addition of cameras to our study system allowed us to document specific behaviors of individual rodents. We found that deer mice appear to avoid each other when possible, perhaps because the most common interactions between individuals are aggressive in nature and could result in physical injury or pathogen transmission (Dizney and Dearing 2013). More aggressive individuals were far more likely to have SNV than less aggressive deer mice (Dizney and Dearing 2013). These results suggest that behavior plays a role in contact and transmission rates. We are currently evaluating the video data to compare behavior with respect to biodiversity.

The importance of contact rates in modeling the prevalence of directly transmitted pathogens cannot be overstated. Our work and that of others demonstrate that density of animals is not always a valid predictor of prevalence, whereas contact rates are constructive in understanding and modeling transmission (Schauber et al. 2015). However, few studies document contact rates, likely because of the perceived difficulty in estimating contacts particularly for small, nocturnal mammals. We have successfully implemented 3 methods (powder marking, PIT tags with antennae, and PIT tags with antennae and video cameras) that vary greatly in initial costs for equipment and labor to estimate contact rates. Powder marking is the least expensive in terms of equipment costs and positive results are indicative of direct contacts. However, it does require extensive trapping efforts, which necessitate a field crew of 3–4 individuals, and the number of animals that can be followed are limited to a handful per site. The PIT tag and

antenna system requires a much larger initial investment than powder marking (~$4,000 per foraging arena) and requires time to deploy and maintain the system. Depending on the amount of activity at the foraging arenas, compiling the data logger results can be time consuming, though this can be done at a later date in the comfort of a field station or laboratory. The results reveal which animals visit a tray, for how long, and if 2 or more animals are in the vicinity of the tray at the same time. Hundreds of visits to trays can be recorded in a single night. The camera system requires additional expenses because it requires infrared cameras (~$150 each) and a computer ($500) that can store the video imagery as well as the software from TimeScience. Since we were using this system off the electrical grid, a generator was required to power the computer. The camera system also is quite labor intensive in terms of deployment and viewing the 8–10 h of video per camera per night. However, the results are unequaled in that one can observe the specific behavior of each visitor to the tray and the nature of any interactions that occur. Each of our 3 systems for estimating contact rates has been extremely valuable in allowing us to begin to elucidate the mechanisms through which diversity impacts pathogen dynamics.

Several new technological advances could greatly enhance research in disease ecology. The monumental increases in DNA sequencing capacity coupled with the significant decrease in costs have the potential to allow investigators to follow pathogen transmission from host to host under natural settings. That is, if the appropriate pathogen is used, investigators could conduct whole-genome sequencing of pathogens to trace transmission patterns. This approach is already being used for humans in hospital settings to understand the transmission and origins of hospital-acquired pathogens. For example, in a recent outbreak of *Staphylococcus aureus*, whole-genome sequencing coupled with a network analysis approach allowed researchers to identify an asymptomatic staff member as the source for repeated outbreaks in the hospital (Harris et al. 2013). In this case, more traditional epidemiological methods had failed to explain the repeated occurrences of this pathogen. It is not too far-fetched to think that in less than a decade, disease ecologists will be able to sequence not only the pathogen but also the host of origin. Such advances will demand new analytical approaches and skills for studying host–pathogen interactions.

In addition, the intense pressure on engineers to produce miniaturized sensors of all types for use in small electronic devices could be a boon to disease ecology research, especially in small mammals. These sensors may afford researchers the capability to monitor free-ranging animals in far greater capacity than ever before. Indeed, some researchers are capitalizing on the existing sensors in cell phones by attaching these devices to free-ranging mammals such as wolves to provide location information (Sekercioglu 2013). It seems probable that in the next decade, sensors small enough to fit on a fingerling-sized ear tag will be available and affordable. The electronics that are currently being produced suggest that these sensors could contain cameras and accelerometers as well as light and temperature sensors. The miniaturization of GPS technology, however, will likely take longer given the current limitations in battery size. Nonetheless, the ability to intensely monitor the environmental parameters of free-ranging mammals, including small ones, holds promise for new opportunities and discoveries in disease ecology and ecology in general.

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Special Feature Editor was Barbara H. Blake.