

Commentary

Harnessing population genetics for pest management: theory and application for urban rats

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Abstract: Effective management of rodent pests requires an ecological understanding of how they move through their environment and how those movements influence the invasion, persistence, or reinvasion of problematic colonies. Traditional methodologies used to describe rodent movement patterns, such as mark-recapture, are hindered by their time-consuming nature and limited geographic scope. As such, our understanding of how rodents interact with urban environments remains limited. Population genetic principles and tools have the capacity to greatly increase our understanding of rodent population dynamics, ecological relationships, and movements across space, but this field is often unapproachable to non-scientist pest management professionals (PMPs). In this commentary, we aim to promote collaborative and integrative rodent pest management by introducing relevant population genetic principles, providing examples of their applications in studies of urban brown rats (*Rattus norvegicus*), and proposing future initiatives that link scientific, private, and government entities. We reinterpret results from a 2018 study of brown rats in Vancouver, British Columbia, Canada to show how genetic relationships among individual brown rats can be used to understand the geographic distribution of genetic clusters (i.e., colonies), natural barriers to migration, and the spatial scale of dispersal. While the 2018 study originally aimed to describe patterns of population genetic structure to understand the influence of urban landscapes on rats, here we describe how these results can be exploited by PMPs to directly inform the creation of management units and decrease the likelihood of rapid post-treatment reinvasion. Further, we discuss the difficulties inherent in population genetic studies and the potential for high-quality model sites to develop generalizable strategies. Overall, we hope to expand the toolbox of PMPs, foster collaboration, and move toward more informed and sustainable management strategies.

Key words: brown rats, dispersal, integrated pest management, population genetics, rats, *Rattus norvegicus*, *Rattus* spp., rodents, urban commensals

COMMENSAL RODENTS, such as the brown rat (*Rattus norvegicus*), are widespread and pervasive pests that pose a danger to public health and infrastructure in both developing and developed countries around the world (Meerburg et al. 2009, Feng and Himsworth 2014, Panti-May et al. 2016). Urban landscapes provide ample human food resources and a diverse array of habitable spaces for rats (e.g., earthen space, underground sewer networks, structural voids within and between buildings), leading to higher population densities of

commensals in cities as compared to non-urban landscapes (Hulme-Beaman et al. 2016). Consequently, urban centers have an increased risk of rat-associated disease outbreaks in people (Himsworth et al. 2013, Leibler et al. 2016). Despite continued efforts by government, private, and academic institutions to control rat populations (Colvin et al. 1996, Channon et al. 2000, Bajomi et al. 2013, Parsons et al. 2017), commensal rodents remain difficult to fully eradicate, and risk of reinvasion or population rebound is high (Davis 1953, Lambropoulos et

al. 1999, Russell et al. 2010, Hacker et al. 2016).

Integrated pest management (IPM) leverages information about the biology and behavior of target pest species to develop tailored management strategies, which are often more effective and more sustainable than traditional rodenticide-focused and non-specific methods. To improve the management of commensal rodents, it is critical to better understand and incorporate the movement patterns and ecology of wild populations. Accurate and high-resolution information on the movement patterns of commensal rodents can provide pest management professionals (PMPs) with several valuable pieces of information that are directly relevant to treatment outcomes. For example, an understanding of group memberships among rat colonies can be used to define eradication units by resolving the number of colonies being targeted, their geographic footprint, and the identification of new immigrants (Robertson and Gemmell 2004, Abdelkrim et al. 2005, Savidge and Pierce 2012). Further, movement patterns can be used to reveal migration patterns across space, particularly natural barriers to migration, which can be exploited as the borders of management units (Combs et al. 2017, Richardson et al. 2017). Understanding movement patterns may also inform PMPs about the relative importance of specific colonies for reinvasion risk and the behavioral underpinnings of movement ecology in rats (Russell et al. 2010, Glass et al. 2016, Puckett et al. 2016). In addition, by determining the spatial scale of dispersal, PMPs can develop buffer zones around specific treatment areas that are informed by target pest biology, lowering the risk of rapid reinvasion.

Current ecological methods for understanding the movements of urban rats to inform management practices are often insufficient. These tools require the capture and identification of individuals in order to track their movements over time. Techniques such as capture-mark-recapture (CMR) are time-intensive, requiring numerous recapture events to resolve movement patterns (Conroy and Carroll 2009). Comparatively, remote frequency identification (RFID) decreases trapping effort by tagging individuals with a unique barcode, which identifies individuals when they approach a sensor (Parsons et

al. 2015). However, both CMR and RFID produce fragmented data, failing to account for movements of individuals between capture events (LaPoint et al. 2015, Byers et al. 2019a). To improve the resolution of movement patterns, very high frequency (VHF) radio-telemetry and global positioning system (GPS) tags can be used to track animals continuously through space. However, radio-signals from VHF tags can be obstructed by structures in urban settings (Lapoint et al. 2015), while GPS tags are difficult to deploy on urban rats due to removal of tags and low recapture rates (Byers et al. 2017). These challenges necessitate alternative methods to understanding rat movement in urban settings.

Population genetics offers a valuable new tool for PMPs in the management of urban rats by using tools from evolutionary biology to track and understand movement dynamics. While these methods have been commonly used to promote movement in species of conservation concern and protect at-risk populations (Schwartz et al. 2006), they can also be implemented in efforts to remove or limit invasive pests (Russell et al. 2010, Fraser et al. 2013, Piernney et al. 2016). Several studies have used population genetics to gain insights on urban rat biology (Gardner-Santana et al. 2009, Kajdacs et al. 2013, Combs et al. 2017, Richardson et al. 2017), but few have described the benefits and challenges of these tools and strategies for PMPs specifically.

Here we discuss the utility of population genetics for improving management strategies of commensal pests. First, we review the basics of population genetic theory and analysis relevant to movement patterns across space, with the goal of providing a primer for interested PMPs. Next, we use a case study from the literature documenting genetic patterns of brown rats in Vancouver, British Columbia, Canada to examine how such information can be interpreted for practical application by PMPs. Then we discuss the future potential and limitations of using population genetics in the context of commensal pest management. Overall, we hope to help bridge the gap between academics interested in urban ecology and the evolutionary consequences of movement and pest managers interested in developing new and informed approaches.

Population genetics for the pest management professional

The field of population genetics measures differences in allele frequencies within and among gene pools over time. Alleles are differences in the genetic code at a particular location in the genome (i.e., a locus) due to genetic mutations (Kimura 1968). These mutations can change a single nucleotide base, creating single nucleotide polymorphisms, or result in new rearrangements of short repeating sequences (i.e., microsatellites). Population geneticists take advantage of these naturally occurring allelic differences to understand evolutionary processes and the ecological mechanisms driving them.

Allelic variation is created through processes of mutation, recombination, and other genomic rearrangements (e.g., duplication or deletion events). Then 3 basic evolutionary forces govern the frequency of alleles in a population: natural selection, genetic drift, and gene flow (Gillespie 2004). Natural selection allows adaptive alleles to rise in frequency because they provide a fitness advantage (i.e., individuals with these alleles have more offspring). Alternatively, natural selection can remove deleterious alleles from a gene pool if they reduce fitness. Genetic drift is a stochastic process that causes alleles to randomly change in frequency, often leading alleles to be lost from the population (i.e., frequency = 0) or become fixed (i.e., frequency = 1). Other examples of genetic drift are bottlenecks, where population size shrinks rapidly, or founder effects, where a small number of individuals found a new population, both of which lead to a random subset of diversity in the resultant population. Gene flow homogenizes allele frequencies among gene pools due to dispersal and subsequent mating that moves genetic information across space (Slatkin 1987). Thus, isolated populations will become increasingly differentiated over time as genetic drift changes allele frequencies in different directions (Holsinger and Weir 2009). Genetic drift and gene flow work in opposition; genetic drift increases with isolation and makes populations more genetically unique, while gene flow increases when populations are more connected (i.e., sharing immigrants) and makes them more genetically similar.

Population geneticists often use models of expected changes in gene pools to contextualize

results. Depending on how data correspond to or differ from model expectations, one can infer the processes that produced the observed pattern of population structure (i.e., extent of genetic differentiation among gene pools). For organisms that exhibit spatially restricted dispersal, a common evolutionary model is isolation-by-distance (IBD; Wright 1943). Under an IBD model, individuals are more related the closer they are in space, and vice versa (Turner 1982). This pattern is expected to occur as short-distance dispersal leads to the build-up of related individuals near one another. Genetic drift acts to remove diversity within each local gene pool faster than diversity can be reintroduced by gene flow due to migrating individuals. In an IBD scenario, geographical distance is a useful predictor of genetic differentiation between individuals, and the degree of genetic change is constant across distance. An alternative model of population structure is used when we expect a strong migration barrier to exist between gene pools, such that individuals on the same side of the barrier exchange genetic information freely, but exchange is limited between individuals on opposite sides of the barrier. This isolation-by-barrier (IBB) model may help to explain genetic variation that cannot be explained by distance alone (under an IBD model). Barriers to migration may completely block gene flow between groups, but more often will restrict gene flow by reducing the number of migrants to a sufficient extent that genetic drift produces identifiable population structure. Analytical tools may look for clusters of genetic similarity to define groups or look for groups that fit patterns of allelic frequencies expected under equilibrium (e.g., Hardy-Weinberg Equilibrium; Alexander et al. 2009). Understanding when wild populations align with model expectations, or how they deviate from such models, can provide insight into ongoing biological processes like movement (Ruiz-Gonzalez et al. 2015).

Management applications from population genetic results

Several recent studies have been published that document patterns of genetic variation among urban brown rats and house mice (*Mus musculus*), where interpretations are geared toward the fields of urban evolution

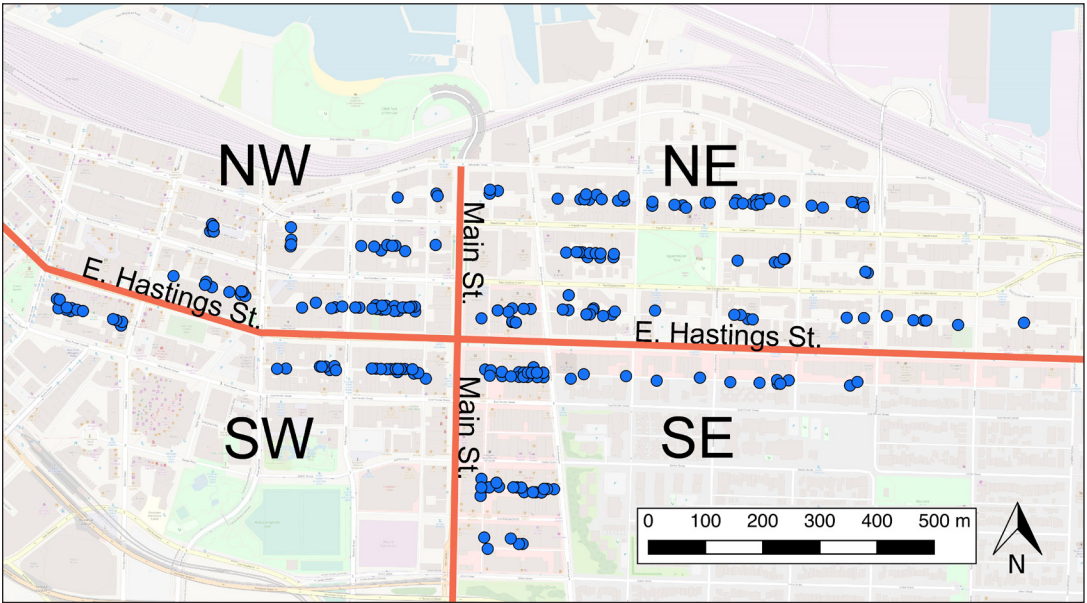


Figure 1. The Downtown Eastside neighborhood of Vancouver, Canada divided into 4 quadrants (Northwest: NW, Northeast: NE, Southwest: SW, and Southeast: SE) by 2 major high-traffic roadways (E. Hastings St. and Main St.). Each blue dot represents the location of a rat ($n = 611$) sampled for this case study.

and landscape ecology (Richardson et al. 2017, Stragier et al. 2019). Here we use a case study in Vancouver, British Columbia, Canada to describe what PMPs can learn from the results of a population genetic study and how this information might be utilized to develop informed and biologically integrated pest management strategies (Combs et al. 2018).

The Vancouver Rat Project is an ongoing public health and urban ecology study focused on rats within a single neighborhood in Vancouver, the Downtown Eastside, and led by this study's co-author (Himsworth et al. 2014, Byers et al. 2019b, Minter et al. 2019). This neighborhood contains many city blocks, each bisected by an alleyway that is vulnerable to brown rat infestation. The neighborhood is divided into 4 quadrants (Northeast [NE]; Southeast [SE]; Southwest [SW]; and Northwest [NW]) by 2 major high-traffic roadways, E. Hastings and Main (Figure 1). Recently, a population genetic study of >600 individuals was published describing spatial patterns of genetic variation (Combs et al. 2018). While there are many potential takeaways from this study, here we reinterpret the results to focus on how patterns of population structure, genetic diversity, migration barriers, and isolation-

by-distance can be used by PMPs for tailored management strategies.

Population structure

Population genetic structure describes the degree of genetic differentiation between 2 gene pools, which can be understood in terms of the number of migrants dispersing between them (Slatkin 1987), though other factors including historical demographic events, natural selection, and mutation rate may also influence contemporary structure (Whitlock and McCauley 1999). Groups that share fewer migrants (or less gene flow) experience stronger genetic drift and thus become more genetically structured from each other. Because genetic structure is due to real differences in allelic frequencies among gene pools, structure allows researchers to identify the origin of individuals based on their genetic makeup (Wasser et al. 2004, Veale et al. 2018). In defining and calculating the extent of structure, researchers can define gene pools to compare ahead of time (*a priori*) based on some expectation of group membership (e.g., frogs from different ponds, rats from different city blocks), or they can allow analyses to group individuals based on the strongest patterns present in

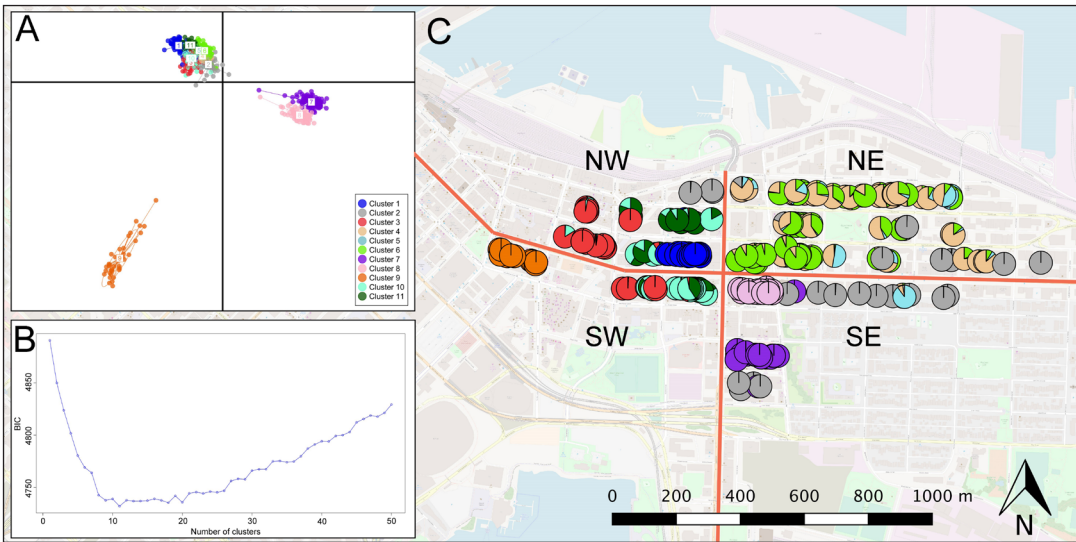


Figure 2. Genetic clustering analysis for Vancouver, Canada rats using Discriminant Analysis of Principal Components (DAPC) reveals closely related colony groups. The DAPC scatter plot describes the genetic similarity among clusters (A). The plot of changing Bayesian Information Criterion (BIC) for different potential numbers of clusters identifies $K = 11$ as the most informative number of genetic clusters (B). The geographic location of each rat's capture is represented by a pie chart indicating the percentage ancestry to each genetic cluster (C).

the data. In the case of rats from Vancouver, researchers used the latter method and describe evidence of multiple genetic clusters (or genetically structured groups) within the single neighborhood (Figure 2). Careful interpretation of the spatial distribution of these clusters and the extent of differentiation can reveal several useful pieces of information for pest managers.

First, genetic structure can help PMPs in their attempts to fully eradicate target areas. For successful management, it is crucial to remove entire colonies because related individuals are expected to share resources and space and because rodent populations can rebound quickly due to their short generation time and large litters (Feng and Himsworth 2014). In Vancouver, genetically structured clusters likely represent 1 colony or several highly related colonies, and they appear to occupy at least an entire city block (Figure 2). This suggests that PMPs should treat rat infestations at the level of the city block when attempting to manage rat activity. This is in contrast to current practices, which often attempt eradication efforts at the level of a single property lot or building.

Genetic structure can also help to identify the sources of new invading migrants (Pichlmüller and Russell 2018). When an individual sample

is assigned to a particular genetic cluster but appears geographically separated from that cluster, it is often assumed that this individual has dispersed away from its natal habitat (emigrated). In this way, population genetics can be leveraged to trace the origins of new invading rats and then target those source colonies to limit future invasions. Such approaches only work if both the source areas and target areas are sampled.

Analysis of population structuring has the power to reveal cryptic differences in movement patterns across a landscape. In Vancouver, brown rats show evidence of 2 contrasting patterns in different quadrants of the neighborhood (Figure 2). Within blocks in the SE, SW, and NW quadrants, genetic clusters occupy 1–3 nearby city blocks, while in the NE, genetic clusters were more diffuse and lacked clear signal of territorial clustering, as evidenced by the lack of genetic structure among blocks. This pattern suggests that colony stability and the extent of movement may differ even at fine-spatial scales. Previous research indicated that rats exist at lower densities in the NE quadrant, which encompasses less stable genetic clusters that appear to experience higher gene flow (Himsworth et al. 2014; Figure 2C).

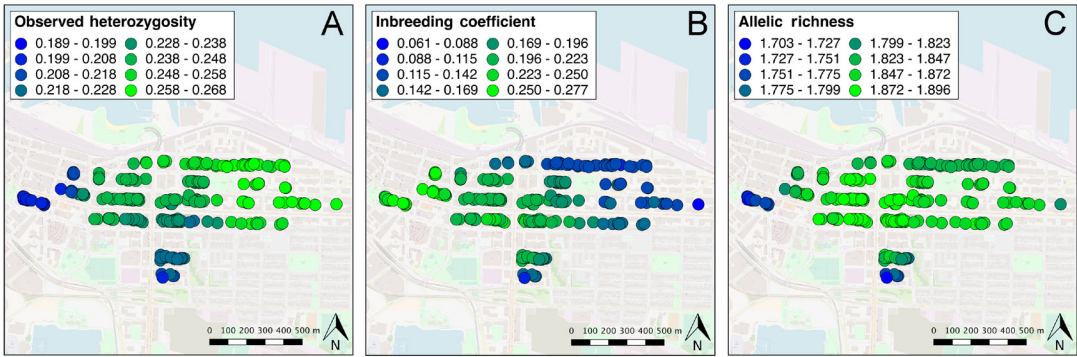


Figure 3. Three metrics of genetic diversity identify differences in movement patterns across space. Observed heterozygosity (H_O ; [A]), inbreeding coefficients (F_{IS} ; [B]), and allelic richness (Ar ; [C]) all vary substantially across only a few city blocks. All diversity metrics were calculated using the sGD software by averaging values in a 300-m buffer window around each sample.

This suggests that rat movement may increase in areas with low rat density. Yet, it remains unclear whether a common environmental attribute is responsible for both low density and high movement among rats, or whether rat movement is attributed to density-dependent factors like territorial behaviors. Thus, PMPs may need to adjust management strategies based on the expected degree of rat movement among blocks, which may be linked in part to resource and rat density.

Genetic diversity

Genetic diversity is directly influenced by the processes of gene flow and genetic drift, which increase and decrease diversity over time, respectively. While often interpreted in conjunction with population genetic structure, analysis of the spatial distribution of genetic diversity can provide insight into movement patterns to inform PMPs about recent behavioral patterns and optimal strategies for efficient pest removal (Gardner-Santana et al. 2009).

There are several widely used metrics of genetic diversity, and we will describe 3 important indices used in the analysis of Vancouver rats. Observed heterozygosity (H_O) describes the frequency with which multiple different alleles are found at a single genomic locus. This occurs because each diploid individual has 2 copies of each chromosome, inherited from the individual’s parents, allowing 2 potential alleles. Higher rates of H_O may indicate both a large panmictic population, or higher rates of reproductive mixing between previously separated groups, suggesting active

exchange of migrants with other areas.

Inbreeding coefficients (F_{IS}) describe the extent to which an individual’s parents are more related than 2 randomly chosen individuals. Higher inbreeding coefficients denote decreased diversity because inbred individuals are more likely to receive the same allele from both parents (i.e., be homozygous) and because the influence of genetic drift increases through this non-random mating (Gillespie 2004). While inbreeding is often evolutionarily unfavorable due to deleterious effects (e.g., inbreeding depression), related individuals are known to regularly breed in rat colonies and other highly social systems (Townsend et al. 2018). High F_{IS} values in rats suggest that those colonies may repel migrants through territorial behavior and may suggest greater colony stability, allowing related rats to persist and build up over multiple generations.

Allelic richness (Ar) describes the total number of alleles found in a given gene pool. Increased levels of diversity provide more opportunities for natural selection to act on standing genetic variation and buffer the effects of genetic drift. Thus, allelic richness reflects a population’s capacity for adaptation and long-term persistence. Pest managers should expect that areas with decreased levels of allelic richness (i.e., low diversity) have lost alleles due to genetic drift and may not receive migrants at the same rate as other areas. Similar inferences can be made from the detection of reduced rates of H_O .

In Vancouver, strong differences in genetic diversity have been detected among rats, further

suggesting evidence of different movement patterns among even geographically proximate rats (Combs et al. 2018). Rats on blocks in the SE, SW, and parts of the NW quadrants show reduced diversity, while rats in the NE quadrant exhibit increased diversity as evidenced by the H_{O} , F_{IS} , and A_r metrics (Figure 3). This suggests that rats in the NE quadrant migrate more often between blocks to reproduce, compared to other rats in different quadrants. This type of understanding can help PMPs to generate more targeted approaches for specific areas. For example, after initial eradication efforts, one might want to increase the number or rate of necessary revisits to control migrants and maintain reduced populations.

Migration barriers

One major goal of IPM is to reduce the rate of reinvasion, or the chance that commensal rodents will return to a target area after eradication campaigns. Population genetics can reveal migration barriers that are often responsible for generating observed patterns of genetic structure, which can be used to the advantage of PMPs by serving as the natural boundaries of eradication or management units. Barriers to animal migration may occur for several reasons: landscape features may physically inhibit dispersal success (Clark et al. 2010), behavioral attributes may lead to avoidance of certain areas (Harris and Reed 2002), or physiological constraints may make dispersing across certain conditions more risky (Lee et al. 2009). By exploiting these natural migration barriers, PMPs can reduce the likelihood of rapid reinvasion.

In the case of Vancouver, high-traffic roads appear to restrict gene flow based on the patterns of genetic differentiation and should serve as useful natural boundaries. By examining the genetic clustering analysis in discriminate analysis of principal components (DAPC), it is clear that the first discriminant function (i.e., scatter plot x-axis) indicated that the 2 clusters from the South-East area were highly differentiated from all other clusters (Figure 2). The second discriminant function (i.e., scatter plot y-axis) indicated differentiation between rats on the far West block and all other rats (Figure 2). Boundaries of these 2 clusters of rats align with 2 high-traffic roads, E. Hastings

and Main streets. High traffic roads have also been identified as movement barriers for rats in other cities (Richardson et al. 2017), though underground connectivity through sewer networks may be equally as important in cities with such infrastructure (Heiberg et al. 2012). By exploiting areas known to limit rat movement as the borders of management units, PMPs may reduce the risk of rapid reinvasion as dispersal across those areas is less likely.

Isolation-by-distance

One of the most critical decisions for pest managers in attempting to eradicate rodents and maintain a pest-free environment over time is the spatial scale at which to conduct treatment or control efforts. By designing a buffer area to be treated around a target area, one can minimize invasion risk, but only if the size of the buffer is relevant to the movement patterns of the pest species. Population genetics can provide insight into the spatial scale of gene flow to provide management recommendations through the use of IBD analysis, the background theory for which is described above (Wright 1943). By analyzing the extent of IBD for pairs of samples within specified distance classes (e.g., relationship between rats caught 0–100 m from each another, 100–200 m, etc.), we can elucidate the extent of local gene flow through a correlogram analysis (Brooks 2003).

A correlogram describing rats in Vancouver suggests that pairs of rats within 250 m of each another show evidence of spatial autocorrelation (Figure 4). This means that beyond 250 m, genetic drift acts to make rats no more related than they would be at random, while within that distance there is evidence of gene flow (i.e., movement) between individuals. This suggests that a treatment area surrounding a target area of at least 300 m might reduce the risk of rapid reinvasion by nearby dispersing rats. Of course, this strategy is not a guarantee that the target area will remain free of new invading rats, but it should reduce the likelihood of, or time until, reinvasion based on the observed migration dynamics.

Rats have shown clear ability to disperse between city blocks, which should be reflected in strategic eradication efforts. Both observation and genetic research has identified that among brown rats, a small but consistent number

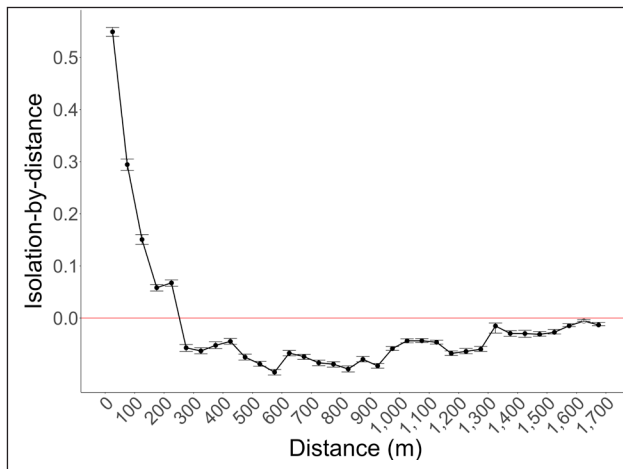


Figure 4. Correlogram analysis for Vancouver, Canada rats indicates a decrease in isolation-by-distance (mantel r value), and thus evidence of local gene flow, as the distance between pairs of rats increase. Past 300 m, rats are no more related to one another than they are to any random individual, while at shorter distances rats are increasingly related, revealing evidence of local dispersal. Distance classes (i.e., groups of rats at specific distances from one another) are presented at 50 m increments.

disperse up to several hundred meters from their natal site (Davis et al. 1948, Davis 1953, Combs et al. 2017), and home range size for male rats increases when searching for mates (Taylor and Quay 1978, Glass et al. 2016). We advise that PMPs should expect occasional movement of rats between city blocks and to treat surrounding areas accordingly. Long-distance movements of >1 city block may also occur at low frequency, particularly following disturbance (Creel 1915), which may be more difficult to mitigate.

Future potential and limitations of population genetics in pest management

Since the mid-twentieth century, pest management strategies have rapidly progressed with the adoption of integrated pest management, which better incorporates the behavior and ecology of target species (Apple and Smith 1976, Singleton et al. 1999, Witmer 2007, Corrigan 2011). Biologically informed strategies are often cheaper, more successful, and create less negative impact on the surrounding environment (e.g., nontarget mortality) than traditional methods relying solely on rodenticides (Brown et al. 2006, Lambert et al. 2008). This commentary demonstrates how

population genetic approaches provide actionable information for PMPs that can be incorporated into IPM strategies without the need for long-term movement monitoring or trap and release methods.

Population genetics reveals ongoing but cryptic movement processes both in urban and non-urban environments (Kajdacs et al. 2013, Varudkar and Ramakrishnan 2015). In fact, genetic approaches to understanding urban rat movement commonly reveal increased movement compared to observational approaches (Byers et al. 2019a). Genetic approaches can be used to identify the parents of rodent embryos and offspring; several studies have shown evidence of multiple paternity in rats and extended home ranges for mate-seeking males (Costa et al. 2016, Glass et al. 2016). Approaches explicitly incorporating landscape features have helped to untangle the complex patterns of genetic structure and diversity across urban landscapes, highlighting how certain environmental aspects might promote or restrict movement (Stragier et al. 2019). Ultimately, genetic monitoring programs, in which at-risk areas are repeatedly sampled over time, may provide the most useful application of population genetics in mitigating rodent pests (Richardson et al. 2019). Monitoring programs can actively assess changes in genetic structure and population size and rapidly identify new invading groups before they establish (Schwartz et al. 2006).

Although we focus on neutral variation (i.e., genetic differences not influenced by natural selection) rather than adaptive genetic changes, population genetics can reveal the influence of natural selection on populations, as has been shown in several urban-dwelling wildlife species (Mueller et al. 2013, Harris and Munshi-South 2017). Such studies of adaptive changes in commensal pests might uncover opportunities for management that exploit natural selection. Perhaps the most controversial use of population genetics for rodent control is the use of gene drives, which could exploit a male-determining gene such that all affected offspring are male, driving the

population to extinction (Piaggio et al. 2017). This technology is still being developed, and the risks of such approaches are still being debated (Gemmell and Tompkins 2017).

In urban settings, even well-designed commensal rodent treatment programs can suffer from a lack of long-term investment and community support. We suggest that academic, government, and private entities should aim to collaborate in efforts to understand and mitigate urban rat populations. Collaboration allows stakeholders to share work, costs, and information, which promotes the integration of results into informed management strategies. Ideally, these projects involve entire communities and allow residents access to relevant information. For example, results from the case study in Vancouver will be shared with the city of Vancouver and British Columbia's Structural Pest Management Association to develop informed strategies and continue collaborative efforts on urban rat surveillance.

Research on urban rats has also been limited by opposing goals of PMPs looking for expedient, sustained removal and scientists looking for model sites for long-term research projects (Parsons et al. 2017). We support the argument of Parsons et al. (2017) that multiple high-quality sites can serve as models from which to develop generalizable strategies and better understand target species biology. Though we present interpretations in this paper specific to Vancouver's Downtown Eastside neighborhood, recent research suggests that dispersal behavior is fairly consistent across different urban landscapes and generates similar spatial patterns of genetic variation (Combs et al. 2018). Thus, results and implications described here may be generalizable for use by PMPs in other specific urban rat contexts.

Yet, treatment strategies for commensal rodents will often require local context, as the natural, social, and structural characteristics of each landscape may create unique conditions for rat movement and control. For instance, on South Georgia Island, natural barriers such as glaciers and bays created useful eradication units for rat pests, while in Salvador, Brazil, topographical features (i.e., individual valleys) were reported to separate distinct evolutionary clusters and provided natural boundaries for eradication (Robertson and Gemmell 2004,

Kajdacsi et al. 2013). In heavily urbanized landscapes, which may lack obvious "natural" migration barriers, different attributes such as roadways, sewer networks, or variable resource availability may be important. In New York City, USA, for example, the Midtown neighborhood, which is associated with fewer permanent residents and increased sanitation, was identified as a soft barrier to migration due to fewer resources and overall lower habitat quality (Combs et al. 2017). Integrated pest management relies on PMPs to evaluate unique aspects of each treatment zone to tailor strategies. Similarly, population genetic results should be interpreted with respect to local landscape idiosyncrasies.

For those engaging in population genetic assessment of commensal rodents, we suggest attaining the greatest possible sample density over a large spatial context (i.e., well outside the expected treatment zone) to better identify potential migrant sources and understand local context. While population genetic assessment presents inherent difficulties for practical use by PMPs—the sample collection, labwork, and computational analyses associated with such projects require significant time, funding, equipment, and training—advances in sequencing technology as well as statistical and molecular methods have opened the door for cheaper, faster, and more accurate population genomic analysis for those with proper preparation.

The use of population genetic tools also necessitates understanding of the temporal aspect of the resulting genetic patterns. Genetic drift requires multiple generations to create clear differences among groups, so assessing recently established populations may be less informative than those that have had significant time to differentiate (Sokal and Wartenberg 1983). Similarly, one should expect a time lag between the initiation of a treatment or habitat modification and any resultant genetic changes (Epps and Keyghobadi 2015). Behavioral flexibility and response to disturbance by commensal rodents should also be noted. Rats may alter movement strategies based on changing resource availability or habitat modifications, and treatment itself may cause increased movements as colonies lose stability due to disturbance.

Conclusion

Given rapid urbanization worldwide and the persistence of rat populations in cities, PMPs are faced with the ongoing challenge of controlling these urban pests. For cities to enact effective rodent control programs, an underlying understanding of local rat population movement and ecology is essential. We have demonstrated that genetic analyses can provide PMPs with relevant biological information for determining local eradication units to better target rat control efforts. We describe the utility of interpreting analyses of population structure, genetic diversity, migration barriers, and isolation-by-distance in the context of urban brown rat management. To resolve local eradication units, we encourage collaborative efforts among PMPs, city officials, and researchers. Future studies identifying movement patterns of individual rats in relation to disease status and landscape features will further resolve rat dispersal dynamics in cities. By demonstrating the utility of population genetics, we hope to open the door to further integration of genetic tools by PMPs for the development of sustainable and informed pest control strategies.

Acknowledgments

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