Supplementary Material

**Rats About Town: A Systematic Review of Rat Movement in Urban Ecosystems**

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Table 1. Details of the literature search procedure

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| Concept | Keyword |
| Urban | urban\* OR residential OR city OR cities OR suburban OR metropol\* |
| AND |  |
| Rats | “*Rattus norvegicus*” OR “Norway rat\*” OR “brown rat\*” OR “*Rattus rattus*” OR “roof rat\*” OR “black rat\*” |
| AND |  |
| Movement | dispersal OR emigration OR expansion OR immigration OR migration OR movement OR boundar\* OR distribution OR domain OR “home area\*” OR “home range\*” OR “site fidelity” OR zone |

Table 2. Number of unique published studies (n = 37) by continent

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| --- | --- |
| **Continent** | **Number of studies** |
| Africa | 31 |
| Asia | 41 |
| Europe | 8 |
| North America | 192 |
| Oceania | 0 |
| South America | 52 |
| Antarctica | 0 |

1 Study site is transcontinental Egypt (Petrie et al., 1923)

2 Multi-city comparison including samples from both North and South America (Combs et al., 2018a)

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| **Table 3.** Relevant details of studies included in a review of urban rat movement (n = 39)  |
| **Study** | **Location** | **Species** | **Sample Size** | **Method** | **Relevant Results** |
| Andrews and Belknap, 1983 | Ralston, NE, USA | Norway | Unknown | Proxy (bait uptake) | * Within six months o­f control efforts, rats emigrated from, and immigrated to, the site of control efforts
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| Angley et al., 2018 | New York, NY, USA | Norway | 100 | Genetics (SNPs) | * Rats in ecologically similar areas were more genetically similar than were rats in different habitat types, suggesting that rats moved among similar habitats (e.g., residential parks vs. mixed-used infrastructure)
* Ectoparasite communities (transmitted among hosts via close contact) were more similar among rats near each other than rats further apart, which may be due, in part, to short-distance movements and interactions among colonies
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| Barnett and Bathard, 1953 | London, England | Norway | Unknown | Proxy(bait uptake) | * Following reductions of rats in two sewers by poisoning (to 10% the size of the population), the population rebounded within six months post-control
* The authors posited that the increase in rat numbers following control was partly due to the invasion of rats from the surface into the sewer
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| Bentley et al., 1958 | London, England | Norway | Unknown | Proxy (bait uptake, dyed feces) | * Rats moved up to 255ft in one section of the sewer
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| Bentley et al., 1959 | England | Norway | Unknown | Proxy (bait uptake) | * Following poisoning, population increases of >3% per week were hypothesized to be due, in part, to the migration of rats from the surface and from adjacent sewers
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| Berthier et al., 2016 | Niger | Black | 230 | Genetics(microsatellites) | * Individuals within the city were more closely related to each other than they were to rats outside of the city
* No evidence for isolation by distance\*\*
* Sites connected by roads were more genetically similar than sites that were not, suggesting potential human-mediated dispersal via roadways and rivers
* Nineteen rats were potential migrants (genetically assigned to an area other than the one of their capture)
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| Byers et al., 2017 | Vancouver, BC, Canada | Norway | 14(tagged)3(recaught) | Continuous (GPS) | * Geographical Positioning System tags were unsuccessful in obtaining rat movement data, which may be due to tag removal by rats and line-of-site obstruction
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| Calhoun, 1948 | Baltimore, MD, USA | Norway | 273 | Capture-Mark-Recapture | * Rats were recaught within 110ft of their initial capture site
* Rats introduced to an unfamiliar block would occasionally emigrate. If the block was near to their home block, an equal number of rats would stay in the new block as would return home (n=6). When rats were released into a block further from their home block, fewer rats were recaught in the block of release, suggesting emigration or mortality
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| Colvin et al., 1998 | Boston, MD, USA | Norway | Unknown | Proxy(bait uptake) | * Rodenticide presence in sewer rats was possibly an indication of movement among the surface and sewers as poisoning was conducted on the surface but not in sewers
* The activity of surface rat populations did not necessarily correspond with sewer rat activity, suggesting that rats did not regularly move between the surface and sewer
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| Combs et al., 2018a | New York, NY, USA;  New Orleans, LA, USA; Vancouver, BC, Canada; Salvador, Brazil | Norway | 1220 | Genetics (SNPs) | * Evidence for isolation by distance\*\* suggested similar patterns of dispersal across cities
* Rats within 500m of one another were generally closely related
* Gene flow indicated movement of rats among city blocks, with infrequent long-distance movements of up to 1.5km in NYC, 1.5km in New Orleans, and 3km in Salvador
* Areas which appeared to disrupt gene flow were a “resource desert” in NYC, major waterways in New Orleans, and roads in Salvador and Vancouver; these areas were hypothesized to serve as barriers to movement.
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| Combs et al., 2018b | Manhattan, New York City, NY, USA | Norway | 262 | Genetics (SNPs) | * Gene flow among adjacent rat colonies supported isolation by distance\*\*
* First order relatives (e.g., siblings and/or parent-offspring) were found 45.3m apart on average
* Restricted movement across the “midtown” area of the city was hypothesized to be due to landscape features or greater pest control efforts in the area
* One rat was suspected of travelling 7.5km, although whether this was anthropogenically-mediated was unknown
* There was no evidence of male-biased dispersal
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| Costa et al., 2016 | Salvador, Brazil | Norway | 446 | Genetics(microsatellites) | * Rats with a high probability of siring offspring (>99%) were found within the same valley as the pregnant female
* The distance between females and males with a high probability of siring offspring ranged from 0 – 149.6m, with a mean inter-parent distance of 70m ± 58m
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| Creel, 1915 | New Orleans, LA, USA | Norway | 292(tagged)163(recaught) | Capture-Mark-Recapture | * Rats released in an unfamiliar, resource-poor environment (warehouse district) travelled twice as far as did rats released into a residential area with greater resources (4 vs 2 miles)
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| Davis et al., 1948; Emlen et al., 1949\* | Baltimore, MD, USA | Norway | 362 (tagged)119 (recaught)Unknown | Capture-Mark-Recapture; Proxy(dyed feces, tracks in snow) | * The diameter of the home range rarely exceeded 100 – 150m and rarely encompassed roads
* >70% of rats were recaught within 40ft of their original capture site, and 87% of dyed feces were found within 50ft of the bait station
* The home range consisted of a narrow area connecting food and harbourage sites; the extent of movement was determined by the proximity of food and harbourage
* Rats did not utilize the whole area of their home range
* Rats changed home range in response to environmental change
* The greatest distance moved by a rat (360ft) was by an adult female
* Males tended to move further distances than females
* Roads posed a barrier to movement (i.e., of 66 surveys of rat tracks in snow, there was only one instance of crossing)
* Rats crossed roads more often when resources were limited (i.e., in eight surveys of rat racks in snow, there were ten cases of rats crossing roads)
* Alleys limited movement, with the majority of bait-dyed feces found on the same side of the alley as the bait station
* Rats did not appear to invade city blocks where trapping occurred, suggesting that trapping did not prompt rat ingress into these blocks
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| Davis and Christian, 1956 | Baltimore, MD, USA | Norway | 156(tagged) | Capture-Mark-Recapture | * Rats were introduced into a new city block to simulate immigration. In blocks with “stationary” populations (e.g., the population was not growing), when the number of resident rats were replaced with a similar number of alien rats, the population remained stationary. When resident rats were replaced with four times as many alien rats, the population decreased by 25%
* In an “increasing” population of rats, replacement of resident rats with a similar number of alien rats resulted in the cessation of population growth. Lactation rate also decreased suggesting that the decrease in growth rate was due, in part, to a reduced reproductive rate
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| Desvars-Larrive et al., 2017 | Gennevilliers, France | Norway | 86 | Genetics (microsatellites) | * Evidence for isolation by distance\*\*
* Evidence for gene flow between rats in an urban park and outside colonies
* Evidence for sex-biased dispersal – females near to each other were more closely related to each other than were males. Further, four first generation migrants which originated from outside of the park were all males
* Movement among the park and surrounding areas was hypothesized because rodenticides were found in park rats, where rodenticides were banned
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| Gardner-Santana et al., 2009 | Baltimore, MD, USA | Norway | 277 | Genetics (microsatellites) | * Evidence for strong site fidelity as 95% of rats were genetically assigned to their area of capture
* Evidence for isolation by distance\*\*
* Most rat movement was generally restricted to a city block (~62m) with individual movements ranging from 30 – 150m
* Relatives were found within 1.7km of each other (~11 city blocks)
* Some rats were genetically assigned from 2–11.5km away from their capture site, indicating infrequent long-distance movement
* The majority of migrants identified were sexually mature adults
* There was no evidence of sex-biased dispersal
* Genetic differentiation between east and west populations coincided with a fast-moving waterway
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| Glass et al., 1989 | Baltimore, MD, USA | Norway | 372 (tagged)107 (recaught)Unknown | Capture-Mark-Recapture; Direct Observation; Proxy(Tracks in snow) | * Of the 107 rats recaught, those in residential areas were recaught 27.3% of the time at the same location while parkland rats were recaught 7.8% of the time at the same location (the number of recaptured rats at each location was not specified)
* Distances travelled in residential areas were generally less than 15m, and restricted to a single alley system
* Rats moved further in parkland (24.7m; n = 64 movements) than in residential areas (13.5m; n = 77)
* Movements derived from tracks in snow in residential areas were longer than determined by capture data (21.6m, n = 39 tracks)
* Rats rarely moved longer distances, with two rats moving >85m and one individual moving 165m in 15 mins (which involved crossing an alley and major roadway)
* Movement was generally between harborage and food sources and was along fences and other cover
* During a 21hr period, rats crossed alleys 80 times more often than they crossed roads (41.5 rats/hr crossed alleys, 0.5 rats/hour crossed roads) – these levels varied depending on levels of rat and human activity
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| Glass et al., 2016 | Baltimore, MD, USA | Norway | 722 | Genetics (microstallites) | * Evidence of strong site fidelity as 97% of rats were genetically assigned to their block of capture
* Four of the 16 unassigned rats could not be assigned to the region of capture
* By genotyping pregnant females, their offspring, and males, they found that females mostly mated with males that did not reside in the same city block
* For half of the pregnant females, offspring were fathered by more than one male; these males resided in the same alley as each other, which was different from that of the female, suggesting that either the female or a group of males traveled to mate
* The average distance between females and their mates was 114.3m (range: 8 – 352.5m)
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| Gras et al., 2012 | Bologna, Italy | Norway and/or black | Unknown | Proxy (bait uptake) | * Surface rat infestations were strongly correlated with surface but not sewer bait uptake, suggesting that surface infestation is not necessarily a reflection of sewer infestation
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| Greaves et al., 1968 | Portsmouth, England | Norway | Unknown | Proxy (bait uptake) | * The mean rate of increase of the population following control efforts was 20% per week
* Re-infestation of sewer sites following control efforts began at the outer edges of the controlled area, which was hypothesized to be due, in part, to rats invading from more heavily populated surrounding areas
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| Hacker et al., 2016 | Salvador, Brazil | Norway | Unknown | Proxy (track plates) | * Rat mark intensity on track plates (an indicator of rat abundance and activity) rebounded within four weeks of an intensive control program
* Trapping of rats in homes also resulted in fewer rats in surrounding houses, suggesting that rats moved among households
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| Heiberg et al., 2012 | Copenhagen, Denmark | Norway | 332(tagged) 213(recaught) | Capture-Mark-Recapture (PIT tags) | * Rats appeared to be confined to the sewers in which they were born, with home ranges within the extent of the sewer
* Average maximum day-to-day movement was 200m
* There was no difference between males and females in distances travelled and males and females moved together in the same areas
* Areas with high to moderate water flow were found to have higher rat activity, potentially signifying foraging sites
* No evidence of movement between two adjacent but separate sewer systems
* One third of rats were caught once, and many of these individuals were caught in manholes linked to smaller sewer lines suggesting that sewer rats may wander long distances or rats from the surface may visit sewers
* No sewer rats were found on the surface
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| Kajdacsi et al., 2013 | Salvador, Brazil | Norway | 146 | Genetics (microsatellites) | * There was no evidence for isolation by distance\*\*
* Evidence for sex-biased dispersal
* The majority of migrants (9/10) were mature males
* There were possible dispersal/migration routes within and across valleys and neighborhoods
* In the second year of sampling (i.e., following trapping and removal of rats in the previous year), some rats were genetically similar to the rats sampled in the previous year, and others were not, suggesting both population replacement and re-colonization of sites by invading rats
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| King, 1950 | Lawrence, KS, USA | Norway | 20 (tagged)8(recaught) | Capture-Mark-Recapture | * Evidence for strong site fidelity with 63% of rats recaught in the same trap (5/8)
* Rats moved among adjacent buildings, with 25% of rats recaught near to or in a building other than the one of their first capture (2/8)
* Rarely, rats moved longer distances, with two rats moving up to 113ft and 404ft
* Alleys seemed to limit the movement of rats, as only one individual was caught on both sides of the alleyway
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| Low et al., 2013 | Christmas Island, Australia | Black (assumed) | 10 (collared) 6 (tracked) | Continuous (VHF) | * Males (n=2) had larger home ranges than females (n=4) which was hypothesized to be due to differences in mate-searching behaviors
* Male average home range size was 1.055ha (KDE) and female average home range size 0.272ha (KDE) for an average home range size of 0.533ha
* Male average core home range size was 0.324ha (KDE) and female average core home range size was 0.09ha (KDE) for an average home range size of 0.168ha
* Male home ranges overlapped with other males and females while female home ranges excluded other females
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| Mangombi et al., 2016 | Franceville, Gabon | Black | 480 | Genetics(microsatellites) | * Evidence for isolation by distance\*\*
* The mean dispersal distance between parents and offspring was 496m
* Low levels of genetic structuring suggested relatively high levels of dispersal
* The Mpassa river which ran through the centre of the city (width = 80m) did not appear to impede gene flow
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| Oyedele et al., 2015 | George Town, Malaysia | Norway | 12 | Continuous (VHF) | * Home range size differed between rats caught in two sites, this was hypothesized to be due to differences in resource availability
* Males had larger total home ranges (n = 6; 241m2 (95% HM)) and core home ranges (n = 6; 23m2 (50% HM))than females (n = 6; total = 19m2 (95% HM), core = 4.6m2 (50% HM))
* Rats moved along the same pathways day-to-day
* Males emerged from their burrows approximately one to two hours before females and returned to the nest at the same time or one hour after females; this pattern differed between the two sites
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| Parsons et al., 2015 | New York City, NY, USA | Norway | 13(tagged)7(recaught) | Capture-Mark-Recapture(PIT) | * Only rats released within 10m of a scanning station returned to the scanning area, rats released further away (e.g., 20m) did not return
* Females were active between 6am to 7pm, while males were active throughout the day; both sexes were less active between 9am and 1pm
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| Petrie and Todd 1923; Petrie et al., 1924\* | El Motiâ, Egypt | Black | 341(trapped)146(recaught) | Capture-Mark-Recapture | * Of the 146 recaptured rats, 53 were caught in more than one house
* Most movements (n = 68) were between contiguous houses
* Broader streets appeared to act as a barrier to rat movement, with only one rat travelling to a nearby community square
* The furthest distance travelled by a rat was 250m
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| Recht, 1982 | Carson, CA, United States | Norway | 4 | Continuous (VHF) | * Home ranges were irregularly shaped, and were determined by the presence of vegetation
* Rats used specific pathways around the home range
* Home range use did not decrease towards the edges
* Home range use varied by individual
* Alternate burrows were used, but rats returned to the home burrow regularly
* Rats altered movement patterns and activity with food availability, human activity, and weather
* Two rats were active during the night and two were active during the day
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| Recht et al., 1983 | City of Orange, CA, United States | Black | 5 | Continuous (VHF) | * Rats were nocturnally phased
* Home ranges were irregularly shaped and did not exceed 30.5m in diameter
* Home range use did not decrease towards the edges
* Rats used specific pathways around the home range
* Alternate burrows were used in response to environmental change (e.g., flooding, construction)
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| Richardson et al., 2017 | Salvador, Brazil | Norway | 706 | Genetics (microsatellites) | * Evaluated relatedness among rats across three valleys
* There was limited movement among study sites, with 79% of movement occurring within the valley of capture
* Migration of rats into valleys ranged from 10 – 29% of individuals
* There was a sharp genetic break between two valleys separated by only 50m; there was a high-traffic roadway running between the valleys which was hypothesized to serve as a barrier to movement
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| Takahashi and Lore, 1980 | NJ, USA | Norway | 235 sightings | Continuous (Direct Observation) | * Activity was greatest two to three hours following sunset and prior to sunrise
* Foraging activity did not appear to be affected by traffic or the presence of a trash compactor
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| Tanaka and Kawashima, 1951 | Kochi City, Japan | Norway | 57(tagged)15(recaught) | Capture-Mark-Recapture | * There was evidence for strong site fidelity; many rats (7/15) did not move between recapture periods (5/9 females, 2/6 males)
* Movement distances did not exceed 40m, and rats moved on average 20m (approximately the space of three to four adjacent houses)
* The time between captures did not influence distances moved
* Males generally moved further distances than females
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| Traweger and Slotta-Bachmayr, 2005 | Salzburg, Austria | Norway | 166 | Capture-Mark-Recapture | * Resource-rich areas separated from other rat habitats by roadways had few rats, suggesting that roadways acted as a barrier to movement
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| Worth, 1950 | Tampa, FL, USA | Black | Unknown | Capture-Mark-Recapture | * Home ranges did not overlap with Norway rats
* Rats remained mostly within the block in which they were originally captured and were recaught within the same building or an adjacent building
* Rats rarely moved across city streets
* Rats inhabited elevated areas (e.g., attics) and they climbed shrubbery, pipes, and wires
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\* Studies are extensions of other included papers, and provide some additional data relevant to the review

\*\* Isolation by distance occurs when populations near each other geographically are more genetically similar than populations further apart as a result of short dispersal distances

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