

The secret life of the city rat: a review of the ecology of urban Norway and black rats (*Rattus norvegicus* and *Rattus rattus*)

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Abstract Norway rats (*Rattus norvegicus*) and black rats (*Rattus rattus*) are among the most prolific and widespread urban pest species in the world. Yet despite their ubiquity, a unified understanding of the ecology of these species in urban habitats eludes us. A comprehensive understanding of urban rat ecology is important for managing rat populations and mitigating the harmful effects that they may have on urban ecosystems (e.g., structural damage, food contamination, and disease spread). The objective of this systematic review and narrative synthesis is to collate, compare, and contrast data from the published literature regarding the ecology of Norway and black rats in urban centers. Themes emerging from the synthesis process, and discussed in detail, include population dynamics, behavior, movement, and environmental influences on rat populations.

Keywords Ecology · Rat · *Rattus* · Urban · Review

Introduction

Norway Rats (*Rattus norvegicus*) and black Rats (*Rattus rattus*) are among the most ubiquitous rodents in the world. They belong to the order Rodentia that comprises of over 40 % of all mammalian species (Wilson and Reeder 2005). Many other species known colloquially as rats belong to a variety of families and genera within the superfamily Muroidea, which also includes gerbils, true mice, and hamsters. Norway rats and back rats,

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members of the subfamily Murinae, are known as Old World rats (Wilson and Reeder 2005). Old World rats and mice differ from New World rats and mice (subfamily Sigmodontinae) taxonomically in their molar pattern by having three rows of cusps instead of two- a more primitive pattern (Nowak and Walker 1991). The genus *Rattus* includes 61 species and is the single largest mammalian genus (Aplin et al. 2003).

The first members of the genus *Rattus* arose around three million years ago in the late Pliocene era and rapidly dispersed across Southeast Asia (Aplin et al. 2003). Their descendants have since succeeded in colonizing all major habitat-types and are found on every continent except Antarctica (Lund 1994).

The ecology of *Rattus* spp. is diverse. While the majority of species favor a sylvatic existence, occupying oceanic islands, forests, and sub-alpine to alpine habitats, five of the 61 species of *Rattus* are considered to be true commensals, as they frequently live in close proximity to humans (Aplin et al. 2003). As generalists, commensal species are remarkable in their ability to quickly and easily adapt to a wide range of environments and resources – an adaptation that has caused significant strife among human populations around the world (Aplin et al. 2003). Of the five commensal species, *R. exulans*, *R. nitidus* and *R. turkestanicus* are found mainly in Central and Southeast Asia, while the distribution of *R. norvegicus* and *R. rattus* is virtually worldwide (Aplin et al. 2003). Interestingly, Norway and black rats are so well suited to close cohabitation with people that they are rarely found in the wild (Aplin et al. 2003). Some have even suggested that these species are obligate pests, since they appear to require humans to sustain their populations (Aplin et al. 2003).

Norway rats originated in northern China (Nowak and Walker 1991) and black rats in India and Southern Asia (Bonney et al. 2008; Nagorsen 2005). Both species spread around the world in association with human transportation, particularly ship traffic (Bonney et al. 2008; Nagorsen 2005). Black rats are most abundant in coastal areas (Bonney et al. 2008) and in the tropics (Nowak and Walker 1991), while Norway rats are better adapted to temperate climates (Nowak and Walker 1991). Additionally, although Norway rats can inhabit rural areas like black rats, they are most strongly associated with urban ecosystems (Yahner 2001).

Norway rats, and to a greater extent black rats, are particularly destructive agricultural pests, causing significant crop destruction, particularly in South and Southeast Asia (Aplin et al. 2003). For example, Norway and black rats have caused chronic losses in traditional rice production systems in the order of 5–10 % of the total crop annually – a volume that could feed more than 180 million people for a year (Singleton 2003). In United States, rats cause an estimated \$19 billion dollars in economic damages annually through consumption and contamination of stored grains (Pimentel et al. 2000, 2001). Norway and black rats are also problematic as an invasive species, and can have devastating effects on natural ecosystems by displacing and reducing native populations of birds, reptiles and plants (Nowak and Walker 1991).

The consequences of rat infestations can be equally severe in urban centers, where rats can cause extensive structural damage, spoil foodstuffs, and result in significant expenditures associated with pest control efforts (Margulis 1977; Marsh 1994; Vadell et al. 2010). Additionally, the urban environment promotes close contact between rats and people (Clinton 1969; Marsh 1994), which can increase the risk of zoonotic disease transmission. Rats are most famously associated with the Black Death (bubonic plague), which killed 40 % of the European population in the 14th century (Perry and Fetherston 1997). However, Norway and black rats continue to be the source of a number of different pathogens responsible for significant human morbidity and mortality in cities around the world, including *Leptospira* spp., Seoul hantavirus, murine typhus, and even *Yersinia pestis* (the causative agent of the plague) (Meerburg et al. 2009). Himsworth et al. (2012) provide a comprehensive review of the zoonotic risks associated with urban rats.

Given unprecedented rates of global urbanization (indeed, over half of the global population now resides in urban areas) (United Nations 2012), urban rat infestations and the issues associated with them will only escalate in the future. It is vital that we understand the ecology of rats in urban centers for a number of reasons. Specifically, this understanding is essential: 1) for the development of efficient and effective rat control strategies; 2) for gauging the public health risks associated with rats, and the measures needed to monitor and mitigate those risks; and 3) to anticipate and track changes in rat populations associated with the ever changing face of the urban ecosystem.

Despite our longstanding cohabitation with rats in cities around the world, a unified understanding of the ecology of this species eludes us. The objective of this review is to aid in the development of this understanding by collating, summarizing, and evaluating published literature regarding the ecology of rats (*Rattus rattus* and *Rattus norvegicus*) in urban centers.

Methods

Computer-based searches of published literature were conducted using the following databases: CAB Direct, JSTOR, BIOSIS Previews, Zoological Records Plus, Web of Science, and Medline. Text word searches using keywords pertaining to rats (*Rattus norvegicus*, *Rattus rattus*, black rat, Norway rat, brown rat, roof rat), ecology (ecology, population, population dynamic, distribution, infestation, habitat, management, harbourage, monitor, behavior, reproduction, environment), and the urban environment (urban, city, cities, municipal, suburban, residential, metropol*). Groups of keywords were combined using the Boolean operator 'AND'. Papers in languages other than English were excluded from consideration. The earliest date cut-off for each database was used to obtain the most complete collection of literature. The search was conducted between November 2011 and January 2012.

The initial literature search yielded 250 sources (including papers and books). All papers that did not focus primarily on rat ecology (e.g., rat control and extermination studies), that involved rat species other than *Rattus norvegicus* and *Rattus rattus*, or that pertained primarily to rural or agricultural situations were excluded. Additional sources were added through citation searching to fill specific information gaps. The final group of 90 papers was reviewed in detail.

The data from these papers was synthesized based on the methodology for narrative synthesis described by Arai et al. (2007). Specifically, preliminary data extraction and synthesis was conducted using grouping of papers by subject, tabulation (i.e., summarizing papers in tables), and thematic analysis (i.e., identification of common themes among included papers). Subsequently, themes were more deeply explored using the process of translation to compare and contrast the contents of the included papers.

All of the below discussion pertains to ecology of Norway and black rats in urban centers.

Results and discussion

The following are the main themes identified through this review and discussed in detail below: 1) population dynamics, 2) behavior, 3) movement, and 4) environmental influences. Although the focus of this review was on rat ecology in urban centers, characteristics inherent to rat populations regardless of location are also included.

Population dynamics

Growth and maturity

Compared to rats residing in rural areas, urban rats generally have a higher growth rate and reach sexual maturity more quickly (i.e., at a relatively smaller size) (Davis 1949, 1951a; McGuire et al. 2006; Perry 1945; Vadell et al. 2010). It has been suggested that this is a result of greater availability of resources in urban vs. rural environments (Glass et al. 1988). Indeed, growth and maturation rates may vary among cities and among different areas within a city as a function of varying resource abundance (Glass et al. 1988). In both urban and rural rats, growth rate declines with age, however, mature urban rats continue to gain mass as they age, whereas mature rural rats either maintain the same weight or lose weight (Glass et al. 1988). Interestingly, Davis (1949) showed that rats from both urban and rural populations grew at the same rate and reached the same size when raised on the same diet. Sex will also influence growth. Specifically, male rats tend to have a higher growth rate and to be larger than females (Glass et al. 1988; McGuire et al. 2006).

Weight and age have a linear relationship only during the earliest portion of a rat's life (Martin et al. 2001). After adult size is reached, weight no longer serves as a useful indicator for chronological age (Martin et al. 2001). Moreover, the exact relationship between weight and age will vary among populations (Davis 1949) due to differences in growth rates as determined by resource availability (Davis 1949, 1951a; Glass et al. 1988; McGuire et al. 2006). In other words, differences in average growth rate and size among distinct rat populations means that the association between bodyweight and age must be determined independently for each population, and that bodyweight can only be used as a proxy for age within the population for which that association has been validated (Davis 1949). Despite its lack of accuracy, bodyweight is often used as a measure of chronological age due to its simplicity and the lack of other suitable and accessible proxies for age (Hardy et al. 1983; Martin et al. 2001; Tamarin and Malecha 1972). Although more laborious to obtain, eye lens weight is, perhaps, a better method of determining chronological age as it is less prone to population-specific variation (Hardy et al. 1983). However, the accuracy of this measure also decreases with the age of the rat because growth of the eye lens slows after maturity, at which point eye lens weight no longer has a linear relationship with age (Hardy et al. 1983). In fact, it has been suggested that this technique is only valid up to 3 to 4 months of age in rats (Birney et al. 1975; Hardy et al. 1983; Myers et al. 1977; Williams 1976). Beyond the 4 months of age, age may, instead, be determined through measurement of the insoluble protein content of the eye lens (Dapson and Ireland 1972; Hardy et al. 1983). An increase in soluble protein content in lens occurs during growth while the conversion of soluble to insoluble protein content in the eye lens occurs during aging after maturity (Dapson and Ireland 1972). Insoluble protein content of the eye lens is a curvilinear function of age, and can be used to estimate age in rodents up to 2 years old (Dapson and Ireland 1972).

Reproduction

The rat gestation period is approximately 3 weeks (Margulis 1977). In urban environments where conditions are favorable, rats may reproduce year round and have as many as 5 litters per year with 4–8 young per litter (Davis 1953; Marsh 1994; Perry 1945; Tamarin and Malecha 1972). Number of litters per year and number of young per litter is dependent on resource availability, which is, in turn, dependent on the environment and the existing

population density (Marsh 1994). Additionally, number of young per litter will increase with the size and maturity of the female (Davis 1951a; Perry and Fetherston 1997).

Female rats living in groups have been observed to establish oestrus synchrony (McClintock and Adler 1978). This synchrony is significant because it can result in coordinated population booms as large numbers of young are weaned and enter the population almost simultaneously (Marsh 1994; Ziporyn and McClintock 1991). Interestingly, among females that reproduce synchronously, approximately 80 % of pups will survive till weaning compared to 28 % pup survival in females that reproduce asynchronously (Ziporyn and McClintock 1991). When pups are born synchronously, there are more lactating females that are able to nurse young and less competition among pups (Ziporyn and McClintock 1991). It is thought that litters born asynchronously have higher mortality rates due to competition from older pups (Ziporyn and McClintock 1991). Asynchronous reproduction is observed most commonly in groups of females with a pronounced dominance hierarchy as dominant females can control oestrus synchrony and suppress pregnancy in subordinates, likely to enhance their own overall reproductive success (Ziporyn and McClintock 1991).

After birth, pups are able to eat solid food as early as 3 weeks of age and can be weaned at 1 month of age (Marsh 1994). Subsequently, reproductive maturity may be reached as early as 3 months of age (Marsh 1994). Rapid maturation and frequent reproduction means that rat infestations may quickly get out of hand if the environment is favorable.

Although urban rats may produce year round, reproductive cycles are not constant. Periods of intensive breeding may occur and will be followed by a 'resting' period (Perry 1945). In temperate climates, variations in reproductive activity have been linked to seasons, with activity peaking in the spring and fall and declining in the winter (Davis 1953; Margulis 1977; Marsh 1988; Tamarin and Malecha 1972). Peak population density tends to occur in the late summer and early fall due to increased juvenile recruitment (Margulis 1977; McGuire et al. 2006; Traweger et al. 2006; Vadell et al. 2010). In tropical climates, seasonal variations in reproductive activity are less pronounced or absent entirely (Davis 1953; Tamarin and Malecha 1972). It is thought that reproductive seasonality is a result of changes in the physiology of the female rats, as males do not appear to show any variation in reproductive capability with season (Perry 1945). Additionally, peaks in reproductive activity appear to be associated with increased pregnancy rates among young females, as large, mature females breed at a uniform rate (Davis 1953).

Mortality

Wild rats have very short life spans. The probability of dying is 90–95 % per year (Davis 1953), meaning that most rats do not survive beyond 1 year of age. Natural lifespan does not appear to vary among geographic locations or habitats (Glass et al. 1988); however, males tend to die at a younger age than females (Davis 1953; Glass et al. 1988; Margulis 1977; Storer and Davis 1953). Although there is little information on the causes of rat mortality, it has been suggested that mortality is primarily a function of resource limitations combined with interspecific competition (Davis 1953; Davis and Christian 1958; Orgain and Schein 1953; Whishaw and Whishaw 1996).

The effect of predation is thought to be negligible in a well established population (Marsh 1994). While cats and owls may prey on rats in urban settings, they do not reduce numbers sufficiently for effective biological control (Marsh 1994). However, if the population is very small or has been eradicated, predators may be able to prevent re-infestation (Marsh 1994). Interestingly, predators, such as cats, tend to kill smaller rats, resulting in the selective removal of juveniles (Davis 1953).

Very little is known about the effect of natural disease on rat populations. The spirochaete *Leptospira icterohaemorrhagiae* and the nematode *Capillaria hepatica* had no appreciable effect on individual or population health despite high prevalence in one study (Davis 1951b). *Salmonella* spp., though found at a lower prevalence overall, produced some mortality, but the population quickly recovered from the outbreak and it was concluded that the pathogen had only a temporary effect on population size (Davis 1951b).

Population size and structure

If the environment is stable, population size also remains constant (Davis 1953; Margulis 1977). Conversely, drastic changes in the environment, such as alien colony introduction or reduced availability of food and resources, will tend to disturb the population equilibrium (Davis and Christian 1956). Natural changes in population size are usually due to changes in young survival rather than changes in reproductive rate (Vadell et al. 2010).

As suggested above, stable rat populations can be significantly altered by the introduction of alien rats (Davis and Christian 1956). Large introductions may disrupt the native population to such an extent that it may cease to grow or may decline in numbers (Davis and Christian 1956). These disruptions, however, are usually short-lived, and the population tends to stabilize and subsequently increase after introductions have ceased (Davis and Christian 1956).

Intensive live-trapping or poisoning of rats has also been shown to alter the size and social structure of a rat colony (Davis and Christian 1958). This is most likely a result of the removal of dominant individuals (which may be more likely to enter a trap or to eat poisoned bait), as well as immigration of rats from adjacent blocks due to the sudden availability of resources (Davis and Christian 1958). However, once trapping or poisoning ceases, the fecundity of rats will cause the population to rapidly return to pre-intervention size (Davis and Christian 1958; Margulis 1977; Vadell et al. 2010; Wundram and Ruback 1986).

Behavior

Feeding behavior and food selection

Black rats preferentially consume fruits, nuts, and seeds (Marsh 1994), while Norway rats, being more omnivorous by nature, will eat a wide array of feedstuffs (Clapperton 2006). Food preference in rats is influenced by previous experience and nutritional value of food (Barnett and Spencer 1953). However, rats are incredibly opportunistic and will adapt to a variety of foods, therefore food selection is largely determined by availability (Traweger and Slotta-Bachmayr 2005). In the case of urban rats, refuse is a source of food for both black and brown rats, particularly in the absence of more natural resources (Glass et al. 1988; Traweger and Slotta-Bachmayr 2005). That being said, most rats will refuse food that is rotten (Glass et al. 1988).

Feeding behavior in rats is best predicted by time taken to consume food, which is, in turn, determined by the size of the food stuff (Whishaw and Whishaw 1996). Small pieces of food (crumbs, flour, wheat, etc.) are eaten directly where they are found, while larger morsels tend to be carried to a secluded area for undisturbed consumption (Barnett and Spencer 1951; Whishaw and Whishaw 1996). Rats generally avoid open areas and tend to feed close to cover (Barnett and Spencer 1953; Barnett 1956; Takahashi and Lore 1980), with the exception of dominant rats, who are more likely to consume food directly at the food source (Whishaw and Whishaw 1996). Large food items are often selected preferentially when both small and large items are available, and rats may attempt to gather and carry multiple food items during a single outing (Whishaw and Whishaw 1996).

Rats have been observed to display strong hoarding behavior in an attempt to avoid conspecific aggression, particularly when hungry or lactating (Clapperton 2006). This trait is also apparently more pronounced in black rats compared to Norway rats (Clapperton 2006). Food carrying behavior, however, may be incorrectly interpreted as hoarding, especially among Norway rats (Takahashi and Lore 1980). Takahashi and Lore (1980) found no evidence of stored food in any of the Norway rat burrows that were excavated. Similarly, no evidence of caching was found among a population of wild Norway rats, although the rats did show a strong tendency towards consuming food in specific locations within their home territory (Whishaw and Whishaw 1996).

Rats are generally nocturnal and most often forage shortly before or at sunset (Barnett and Spencer 1951). Whishaw and Whishaw (1996) and Takahashi and Lore (1980) found that the majority of rat activity tends to occur before 12 a.m., after which very few rats are sighted (Takahashi and Lore 1980; Whishaw and Whishaw 1996). Younger rats, however, may forage earlier in the day to avoid competition from older, larger rats (Whishaw and Whishaw 1996). Rain and inclement weather have been reported to discourage outdoor rat activity (Frantz and Comings 1976; Whishaw and Whishaw 1996), while presence of humans does not appear to disturb rats or alter their feeding patterns (Takahashi and Lore 1980; Whishaw and Whishaw 1996).

A wild rat may visit a food site several times a night (Clapperton 2006; Inglis et al. 1996), however, there are significant sex-related differences in foraging behavior (Inglis et al. 1996). Females forage in many short visits, while males will forage less frequently but for longer periods at a time (Inglis et al. 1996). Pregnant and lactating females, however, will consume larger meals and feed for longer than males (Clapperton 2006). Total amount of food consumed does not vary significantly by sex but is more dependent on the body weight of the rat (Inglis et al. 1996) and the caloric value of the food (Barnett 1963). Overall, rats will adjust their feed intake to meet individual energy demands.

Rats display exploratory behavior while foraging (Barnett and Spencer 1953). This behavior allows rats to collect information on local topography, as well as the whereabouts of food, water, and shelter (Barnett 1956). Rats also show a tendency to sample food, approaching a new source cautiously before retrieving a morsel and making a rapid retreat (Whishaw and Whishaw 1996). It is through this sampling behavior that food associations are learned (i.e., whether a food is nutritious or toxic) (Barnett 1956), and rats will display this behavior regardless of circumstance, age, or sex (Barnett 1956).

In addition to exploration and sampling, some have suggested that rats are able to learn about the safety and appropriateness of different food stuffs by observing conspecifics (Noble et al. 2001). For example, young rats have been reported to learn what is and is not safe to eat by imitating the food preferences of their mother (Clapperton 2006; Marsh 1994), while more mature rats may follow odour trails left by other rats to find safe food (Clapperton 2006). Barnett (1956, 1951), however, argued against social and parental learning as he observed that personal experience and associative learning, particularly due to physical reactions to different feedstuffs, are the primary drivers of dietary preference in rats.

Neophobia

Neophobia is a strong and consistent behavioral characteristic among rats (Barnett 1956) and one that presents a major obstacle for rodent control and management. Neophobia is the fear of novel stimuli, and manifests as avoidance of new food or situations (Mills 2010). It is an adaptive behavioural response that encourages survival of cautious creatures (Breed and Moore 2011; Mills 2010). Degree of neophobia will vary between species, among populations of the same species, and among individuals (Clapperton 2006). Although neophobia may occur in a

number of different contexts (e.g., involving unfamiliar objects, sounds, situations, etc.), most studies of neophobia in rats have focused on neophobia towards food, therefore the following section pertains primarily to food-associated neophobia.

Food choices in rats are influenced by the opposing effects of exploratory drive and neophobia (Barnett 1956) and degree of neophobia is, in part, determined by the level of lethality in environment (Noble et al. 2001). It has been suggested that the highly developed neophobia observed in both Norway and black rats have evolved as a response to intense human control (Inglis et al. 1996). For example, as the amount of poisoned food in the environment increases, rats become less likely to sample novel food and more likely to pay attention to the eating habitats of others (Noble et al. 2001). In high lethality environments (i.e., instances of poisoning with rapidly and/or highly lethal substances), however, there is less opportunity for the development of learned food aversions (Noble et al. 2001).

Interestingly, although neophobia will be exhibited in novel environments, the strongest avoidance behavior in rats is elicited by unexpected object (e.g., a new food container) within a familiar environment (Hardy et al. 1983; Inglis et al. 1996; Marsh 1994). Rats in a familiar environment tend to sample novel food stuffs within the first feeding period (i.e., within 24 h) (Barnett 1956). However, if presented with a familiar food in a novel container, it may take several days before rats are willing to feed from the new container (Barnett 1956; Inglis et al. 1996).

Despite their strong neophobic tendencies, the urge to avoid new objects and conditions is usually overcome relatively quickly due to the adaptive nature of rats, particularly under conditions of hunger and scarce resources (Barnett and Spencer 1951). Moreover, the strength of neophobic response will vary with the stability of the familiar environment (Inglis et al. 1996). Specifically, if a rat's familiar environment changes constantly, then that rat will be less likely to display a neophobic response to new situations (Inglis et al. 1996).

Social interactions

For a species that exists in social colonies, rats display a surprising lack of co-operative behavior (Inglis et al. 1996). On the whole, rats tend to ignore other members of their own colony except when mating occurs, or when sleeping in groups in the nest (Barnett and Spencer 1951). Fighting is relatively commonplace with disputes being more likely to occur over an oestrus female than over food resources (Barnett and Spencer 1951; Ziporyn and McClintock 1991). Although intra-specific aggression has been observed during communal feeding periods, these bouts are usually short-lived, and aggressive advances may even be ignored by conspecifics (Barnett and Spencer 1951). That being said, high population density and diminishing access to resources may increase and exacerbate episodes of aggression (Whishaw and Whishaw 1996).

When fights do occur between wild rats, weight appears to be a major determinant of victory in males but not females (Ziporyn and McClintock 1991). Indeed, when one rat interferes with another in an established colony, the heavier rat may simply push the lighter one out of the way (Barnett and Spencer 1951). For both sexes, however, the rat that initiates a fight is most likely to win that fight (Ziporyn and McClintock 1991).

Fighting behavior is also influenced by dominance hierarchy. Subordinate rats are markedly submissive to dominant rats and are likely to flee, back down, or freeze in the event of a confrontation (Ziporyn and McClintock 1991). Dominance also plays an important role in population regulation (Storer and Davis 1953), as the relative social standing of a rat within its population hierarchy will determine its level of access to resources and mates (Marsh 1994; Orgain and Schein 1953; Whishaw and Whishaw 1996; Ziporyn and McClintock 1991). Dominance can be established through a variety of behaviors including

fighting, controlling access to food and water, and even by passing or crawling over subordinate rats (Ziporyn and McClintock 1991).

The behavior of dominant rats influences the behavior of other rats in the colony (Barnett and Spencer 1951; Calhoun 1962; Whishaw and Whishaw 1996; Ziporyn and McClintock 1991). Dominant rats often occupy the best microhabitats and feed whenever they like, while subordinate rats are relegated to marginal habitats and tend to feed when dominant rats are not present (Clapperton 2006; Marsh 1994). Although rats are generally nocturnal, subordinate rats may be forced to forage during the day in order to avoid competition with dominant rats (Clapperton 2006; Whishaw and Whishaw 1996). Dominant rats may also act as the ‘pioneer’ rat of their colony, and be the first to inspect new conditions or new objects in a familiar environment (Barnett and Spencer 1951). As mentioned above, dominant females have been observed to control oestrus synchrony in the colony, suppress pregnancy in subordinate females, and intercept males approaching subordinate females during group mating (Ziporyn and McClintock 1991). Interestingly, both male and female rats form dominance hierarchies among members of their own sex (Ziporyn and McClintock 1991). However, a dominant female Norway rat may even deter males from using the same food source (Clapperton 2006).

Dominance hierarchies also affect foraging behavior. For example, in order to avoid conspecific aggression, these subordinate rats may carry their food to protected areas where they can eat in peace away from others (Whishaw and Whishaw 1996). It is uncommon for rats to engage in food carrying for the co-operative benefits of others in the nest (Whishaw and Whishaw 1996). In fact, other rats will attempt vigorously to steal food carried home by conspecifics (Whishaw and Whishaw 1996).

Immigration of alien conspecifics into an established colony is also apt to arouse antagonism and, more often than not, results in the immediate ejection of the alien rat from the nest or food source (Barnett and Spencer 1951). Immigration events, however, may also cause drastic alternations to population equilibrium and result in a high incidence of mortality for both the native and foreign rats (Calhoun 1948). That being said, invaders that survive the initial upheaval are usually incorporated into the population and can breed successfully (Calhoun 1948).

With regards to inter-specific competition, size does matter. Due to the relative larger size and more aggressive nature of Norway rats, invasion of Norway rats into black rat territory usually forces black rats to abandon their nests and take refuge on higher ground, such as roofs, pipes, and upper floors of building (Barnett and Spencer 1951; Nagorsen 2005; Nowak and Walker 1991). Although both species have been observed to be able to feed together, the displacement of black rats to higher places likely restricts their access to a number of resources on the ground (Barnett and Spencer 1951). Indeed, Norway rats may completely displace black rats where the two species coexist, with the marginalized black rats being maintained only in ports through periodic introductions (Barnett and Spencer 1951). Due to the exclusion of black rats from favorable habitats by Norway rats, black rats have been declared endangered in many areas (Lund 1994).

Movement

Barriers to rat movement

The distribution of rats in an urban environment depends on environment suitability, as well as the presence of barriers to rat movement. City streets are among the most significant barriers and tend to separate rats into isolated populations with a population’s home range being limited to a city block (Davis 1953; Emlen et al. 1949; Margulis 1977; Traweger et al.

2006; Traweger and Slotta-Bachmayr 2005). The physical separation caused by streets may result in considerable heterogeneity in rat distribution even over short geographic distances within a city (Gardner-Santana et al. 2009).

Home range

Barriers to rat movement cause the home ranges of urban rats to be very small when compared to rats living in rural areas (Traweger et al. 2006). There are other factors, however, that influence home range size. For example, males may extend their home range during the breeding season when in search of an oestrus female (Clapperton 2006). Availability of food and proximity of burrows to food sources may also determine home range, with range expanding as resources become scarce or more distant (Clapperton 2006). Conversely, in resource rich areas, rats tend to exhibit high site fidelity and smaller home ranges (Gardner-Santana et al. 2009).

Although often confined to a city block, a rat's home range often encompasses more than one dwelling or property at any given time (Easterbrook et al. 2005). Indeed, Glass et al. (2009) reported that rats in urban alleyways will tend to utilize the entire length of that alley.

Dispersal

Despite their small home range, dispersal of rats over short distances is not uncommon and is often successful in urban settings (Easterbrook et al. 2005). Long distance dispersals are more uncommon and tend to occur as a result of extreme resource limitation, high intraspecific competition, and/or drastic environmental change (Gardner-Santana et al. 2009; Storer and Davis 1953).

Environmental factors affecting rat populations

Climate and season

Climatic factors influence the global distribution of rats, with Norway rats and black rats being best suited to temperate and tropical climates, respectively (Cavia et al. 2009; Marsh 1994).

Within a climatic zone, season may also exert an influence on rat populations. As mentioned previously, seasons may influence reproduction (Davis 1953; Margulis 1977; Tamarin and Malecha 1972). However, season may also affect rat activity independent of reproduction. For example, during the winter, inclement weather may cause outdoor rats to move indoors in search of shelter (Frantz and Comings 1976). Indeed, some suggest that it is this seasonal migration that is responsible for increased rat-related complaints from the public during the winter months (Margulis 1977). Curiously, growth rates in urban rats tend to be higher during the winter compared to the summer, while the reverse is true for rural rats (Glass et al. 1988). This winter 'growth spurt' has been attributed to decreased competition (and thus increased access to food) resulting from an overall decrease in population size during the winter, as well as decreased putrefaction of refuse (an important food source) due to colder ambient temperatures (Glass et al. 1988).

Urban environment

Rats actively select certain habitats within a city depending on the availability of adequate harbourage, food, and water (Masi et al. 2010; Sacchi et al. 2008).

Among these three factors, food availability is thought to determine the carrying capacity of a habitat (i.e., the maximum number of animals that that habitat can sustain) (Orgain and Schein 1953). In urban environment, food and organic waste that are improperly stored or disposed of constitutes the most significant food source for rats (Promkerd et al. 2008; Traweger et al. 2006). Interestingly, presence of domestic animals at a residence may also attract rats due to the fact that pet food is often left out for long periods of time and may be easily accessible (Sharp 2007). Although access to water has received less attention in studies of rat ecology, it is no doubt an important factor, as rats require daily access to fresh water for survival (Sacchi et al. 2008).

While food may determine the size of a rat population, the availability of harborage will determine whether a population is able to become established in the first place (Masi et al. 2010). Masi et al. (2009) showed that a premise is 24.2 times more likely to become infested when that structure is easily accessible to rats. While black rats tend to enter these structures through holes in the roof, cracks in walls or ceilings, or access points near utility lines (Masi et al. 2009; Marsh 1994), Norway rats tend to enter structures through sewage systems, as well as cracks or holes in a building's foundations (Masi et al. 2009). Although rats will cohabit with people, abandoned structures are preferred, and may serve as a source of infestation within a block (Childs et al. 1998; Kosoy et al. 1998).

Norway rats may also create their own harborage by burrowing. Indeed, studies have found that the presence of natural soil is a strong predictor of Norway rat populations (Cavia et al. 2009) and that Norway rats are uncommon in heavily built up areas of a city where there is little natural soil available for burrowing (Traweger and Slotta-Bachmayr 2005). Black rats, on the other hand, are more adept at scaling vertical structures and creating nests out of artificial materials, and are therefore common in areas with high building density (Cavia et al. 2009).

Unfortunately, suitable harborage and food sources for rats tend to be most abundant in neighborhoods of lower socioeconomic status; for this reason, these areas are often disproportionately afflicted by rat infestations compared to more affluent areas within a city (Easterbrook et al. 2005; Omodu and Ati 2010). These neighborhoods tend to be older and have a higher proportion of properties that are unkempt, dilapidated and abandoned (Langton et al. 2001). Additionally, impoverished neighborhoods tend to suffer from inadequate public services, including waste disposal, leading to creation of unhygienic environments that are likely to provide food for rat populations (Margulis 1977). Indeed, studies have shown that improved sanitation and structural repairs will result in decreased rat infestations (Davis 1953). The presence of rats in poor neighborhoods does not go unnoticed, and, residents of these neighborhoods often possess a rich folklore regarding the behavior of rats, as well as the best methods to control or eradicate them (Wundram and Ruback 1986). In richer neighborhoods where infestations are less common, citizens often lack awareness or knowledge about rats (Wundram and Ruback 1986).

Conclusions

Previous studies have provided a wealth of information regarding the ecology of Norway and black rats in urban centres. There is, however, a number of remaining knowledge gaps which should be addressed through future research. For example, while many studies have analyzed rat reproduction (Davis 1953; Marsh 1994; Perry 1945; Tamarin and Malecha 1972), the reason behind the short life expectancy of rats and the natural causes of rat mortality remain a mystery. In particular, the effect of natural disease on rat populations has

not yet been explored. Additionally, although we are familiar with the basic requirements of rat populations (i.e., food and harborage), the exact features or combination of features of the build environment (i.e., the parts of the urban environment determined by human design) that promote or deter rat infestations remains unclear. This type of knowledge would be useful for municipalities so that they may take rodent control into consideration during city planning and management. Finally, given that rats are a potential source of disease for humans, the effect of rat ecology on pathogen transmission among rats and the risk of pathogen transfer to people is a topic warranting further study.

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