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Urban Social Insects

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Urban areas cover nearly 3% of the Earth's land surface, an area that is expected to triple in coming decades. Increased urbanization, along with climate change and the spread of invasive species, has been identified as a primary cause of biodiversity loss. But at the same time, recent studies have found that cities can serve as reservoirs for biodiversity, especially for some social insects. Even in a city the size of New York (population 8.6 million), ants outnumber humans 2000 to one, and more than 40 ant species can be found within a ten-mile radius of the Empire State Building [1]. Likewise, urban habitats host a diversity of bees, wasps and termite species that take advantage of urban food sources and nesting sites [2]. While many of these species are considered pests, they also provide valuable ▶ ecosystem services that include ▶ pollination, nutrient cycling, and refuse removal.

Urban Ants

Ants have lived in cities for millennia, with early Greek and Roman authors offering home remedies for keeping household ants at bay [3]. As human populations expanded, so too did populations of urban ants. Ants have moved from city to city along both ancient and modern trade routes, and now many urban species have cosmopolitan distributions that cover multiple continents. The success of urban ants has led to a multibillion-dollar industry devoted to the control of pest species, yet only a fraction of the world's urban ants are considered pests. Today's cities are home to a diverse mix of both native and introduced species.

In North America and Europe, over 150 ant species have been identified as common in urban environments [4, 5], and in tropical regions a single city can be home to over 100 different species. Some of these ants are widespread and have popular names that highlight their urban lifestyle, such as the "odorous house ant" and the "pavement ant." But other urban ants are rare and go unnoticed for decades. A new species from the rare ant genus ▶ *Leptanilla*, for example, was discovered in 2018 in the heart of downtown Macau, the most densely populated urban area of the world. Even the pavement ant, one of the world's most broadly distributed urban ants, was recently found to be a cryptic species; its scientific name has now changed from *Tetramorium caespitum* ("grass-living") to the more appropriate *Tetramorium immigrans* ("immigrant").

Although urban ant communities can be diverse, they tend to be dominated by a select group of urban specialists with a range of

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Urban Social Insects, Fig. 1 Pavement ants (*Tetramorium immigrans*) feeding on a dropped cookie crumb. Human foods form a significant portion of the diet for many urban insects, and pavement ants are among the most prolific feeders on human litter and garbage. (Photo by Lauren Nichols)

physiological and behavioral traits that facilitate their adaptation to urban environments. Cities are generally hotter and drier than surrounding habitats due to the urban heat island effect, and urban ants tend to be more heat tolerant than their rural counterparts. Some urban species actually take advantage of urban heat by nesting under hot pavement, thus accelerating the growth of their brood.

Aside from temperature differences, cities are also characterized as high-disturbance habitats, and species that thrive in urban environments are often disturbance adapted. This may be one reason why urban species perform poorly outside of cities, where disturbance levels are low. Urban habitats also feature novel resources, such as human foods (Fig. 1), which provide a massive potential energy source for those ants that are able to exploit them [6]. Some of the most successful urban ants rely heavily on human foods and may even serve as strong competitors with other urban wildlife [7].

The traits that facilitate the success of urban ants were long assumed to be pre-adaptations, but there is now evidence that some ant species are rapidly evolving in response to urban conditions. A growing number of studies have found that plant and animal populations experience divergent selection between urban and nonurban environments, and for ants, the focus has been on temperature. As noted above, cities are warmer than surrounding area, and urban ants tend to have higher thermal tolerances. In a study on acorn ants, ► *Temnothorax curvispinosus*, urban populations were found to have rapidly evolved higher thermal tolerance in response to urban warming [8]. The long history of ants in cites suggests that other traits are likely to have evolved in response to urban conditions.

Among the ants that thrive in urban environments, three deserve special mention: the Pharaoh's ant, the odorous house ant, and the pavement ant. The ► Pharaoh's ant, *Monomorium pharaonis* is considered the most ubiquitous house ant in the world [9]. By the 1860s, Pharaoh's ants had already spread to every continent except Antarctica and had become well-known pests of human dwellings. They are notorious pests of hospitals, where they serve as disease vectors for microbial pathogens. Like many other invasive ants, Pharaoh's ants form ► supercolonies with hundreds of queens that show little aggression among neighboring nests. Their name was given to them by Linnaeus in 1758, who named them after the Egyptian pharaohs because the type specimen came from Egypt. However, the species is now thought to have originated in tropical Asia, and the type specimen Linnaeus described was likely from an introduced population that had arrived in Africa through human transport. Still, the word "pharaoh" in Egyptian means "great house," which is fitting for one of the world's most ubiquitous house ants.

In North America, the odorous house ant, *Tapinoma sessile*, competes with the Pharaoh's ant for the title of the most ubiquitous house ant.

Their name is derived from their house-living nature as well as the curious odor they emit when crushed, which is derived from similar compounds as blue cheese [10]. A similar odor is produced by another house-infesting species, the ▶ Argentine ant, *Linepithema humile*. While the Argentine ant is a global pest, the odorous house ant is somewhat unique in that it has become a pest within its native range in North America. Urban populations of odorous house ants have very different life history characteristics than their rural populations. In rural settings, colonies are small with one or a few queens, and an entire colony often fits inside a single acorn. But in cities, odorous house ants become supercolonial and reach massive colony sizes with thousands of queens. The factors that trigger this change are unclear, but it has likely facilitated their success in urban environments.

Any discussion of urban ants would be incomplete without mention of the pavement ant, *Tetramorium immigrans*. Along with pigeons, rats and cockroaches, pavement ants are among the most common urban animals. They originated in Europe but have now colonized cities from Paris to San Francisco, with populations extending as far south as Buenos Aires in South America. As their name suggests, pavement ants build their nests under paved surfaces and rarely invade buildings. Unlike other common urban ants, pavement ant colonies contain only a single queen and are highly territorial. Each spring, colonies emerge from winter diapause to reestablish territorial boundaries, and large battles are a common sight on city sidewalks during this season. Pavement ants are also voracious eaters of human foods, consuming an estimated mass equivalent to 60,000 discarded hot dogs per year in New York along Broadway alone. For this reason, pavement ants have been considered a beneficial urban species due to their role in refuse removal.

Urban Bees

Cities can also harbor diverse populations of bees [11]. Toronto, for example, claims more than 360 bee species, 90% of which are native to the region. While bees do poorly in the most urbanized parts of cities where pavement cover is high, they thrive in remnant parks and urban gardens. Compared to agricultural lands, which are increasingly planted as monocultures, cities contain a diverse mix of native and introduced flowering plants, as well as lower levels of pesticide residues. For these reasons, cities have been identified as potential refuges for bees and other pollinators [12].

Urban habitats support a mix of both social and solitary bees, although social species do especially well in cities. Cavity-nesting bees can reach high abundances in cities due to the high availability of nesting space in built structures [13]. Urban habits also tend to be dominated by pollen generalists that can take advantage of flower species that are commonly planted in cities. Both of these factors have helped the ▶ western honey bee thrive in urban habitats to the point that there is now concern that honey bees might negatively impact native bees through competition. Social ▶ stingless bees, too, have been found to do well in tropical cities, such as *Melipona* in Brazil and *Tetragonula* in Australia. For ▶ bumble bees, evidence for the impacts of urbanization are mixed, but colonies of some species, such as *Bombus terrestris*, exhibit higher growth rates and reproductive output in cities than in surrounding areas.

Another group of bees that does well in cities is the ▶ large carpenter bees (*Xylocopa*), which in the United States rival termites as destroyers of structural timbers. Carpenter bees use their strong mandibles to bore holes into dead wood to create nest burrows. The prevalence of dead wood in human structures makes urban areas attractive habitat for carpenter bees, and anecdotal reports suggest that some urban populations now favor milled wood over natural substrates.

In addition to wild bees, cities have seen a resurgence in honey bee colonies within their limits as a result of renewed interest in urban beekeeping [14] (Fig. 2). While honey bee colony losses have accelerated over the past 50 years due in large part to the global spread of ▶ parasites and pathogens, urban beekeeping is on the rise. What began as an underground movement to tend rooftop hives has grown into an officially sanctioned

Urban Social Insects, Fig. 2 Urban bee hives on the roof in downtown Durham, North Carolina. Urban beekeeping has rapidly grown in popularity as more American cities have passed laws to allow it within their limits. (Photo by Lauren Nichols)

pastime: New York legalized beekeeping in 2010, Boston in 2014, and Los Angeles in 2015. First Lady Michelle Obama even installed honey bee colonies at the White House in Washington D.C. in 2009.

Interest in urban beekeeping has been so successful that there have been concerns that there are now more honey bees in cities than urban green spaces can support. These concerns have been fueled by reports of bees feeding on waste sugars from human sources, which could impact the bees' health and honey quality [15]. In 2010 a mysterious red honey was found in hives in New York. When tested, it was found to contain large amounts of food coloring from sugar syrup that the bees were collecting from a nearby factory. Two years later, multicolored honey appeared in bee hives in France after the bees had foraged on sugar residues from a candy factory. Despite these anecdotes, research on urban bees in the United States has found that colonies seem to rely on flowers as their primary source of nutrients [15], although bees in the world's largest cities have yet to be investigated.

Urban Social Wasps

Among the social wasps, colonies of ▶ yellowjackets, ▶ hornets, and ▶ paper wasps are the most common in urban environments. Many wasps take advantage of human dwellings to construct their nests under protected eaves or in cavities [16]. While arguments used to promote urban green spaces usually focus on ecosystem services provided by wildlife, increases in urban wasps have actually been categorized as an "ecosystem disservice." Yet wasps do provide valuable ecosystem services in cities, and their negative profile is largely undeserved

Certain wasp species are more likely to take advantage of human structures as nest sites compared to natural settings. Colonies of two paper wasp species, *Polistes fuscatus* and *P. exclamans*, have each been found to nest preferentially on human-built structures, and colonies of the yellowjacket *Vespula germanica* nest primarily on human structures within their introduced range. Some *Vespula* species, such as the southern yellowjacket *V. squamosa*, have been noted for building massive nests in urban settings that contain hundreds of thousands of cells and fill cavities inside abandoned cars, sheds, and attic spaces. Removal of these nests is a primary service provided by pest control companies.

Why some wasps prefer to build their nests on or near human structures is not completely understood. *Polistes* colonies in urban Illinois had higher parasite loads than their rural neighbors, and nests on the sides of buildings are thought to be more exposed to attack by predatory birds. However, some evidence suggests that ant predation on wasp nests is lower for those built on human structures compared to those on vegetation, and human structures may also provide improved shelter from adverse weather. Like ants and bees, urban wasps also take advantage of human-derived food sources, such as sugars present in litter and garbage. There is evidence that some wasps even rely on litter to supplement colonies around the end of the growing season when flowers and other natural carbohydrate sources become scarce.

While public opinion of bees has reached an all-time high due to concerns for pollinator health, wasps continue to be vilified and treated as pests. A recent survey of Tokyo residents found that roughly 80% “dislike” or “rather dislike” wasps, and nearly two thirds said they would call an exterminator to remove a wasp nest even if it had caused no damage or harm [17]. Despite this bad reputation, social wasps play important ecological roles and contribute valuable ecosystem services in urban areas. They prey on many insects, including defoliating caterpillars and other pests of urban trees. Wasps also serve as food for other urban animals, such as birds, and they have an important role in urban food webs. And although bees get most of the credit for pollination, wasps also feed on flower nectar and serve as important pollinators.

Urban Termites

Termites have been the focus of more research in urban systems than probably any other social insect due to their status as major ► structural pests. In natural habitats, termites feed primarily on dead or decomposing plant matter, but pest species move into homes and buildings to feed on lumber and other wood-based structural components [18]. In 2010, it was estimated that termites caused $40 billion in damage worldwide due to the costs of controlling them and of structural repair. While more than 3000 termite species have been described, 183 are recorded as pests in urban environments, and only 79 of these are considered serious pests. Research on urban termites has focused predominantly on these few pest species, and much less is known about termite diversity or the biology of non-pest species in urban environments.

Pest termites are often classified based on their nesting habits into three categories: dampwood termites, drywood termites, or subterranean species. Of these, ► drywood termites and ► subterranean termites contain almost all common pests. Drywood termites (Kalotermitidae) have relatively small colonies that are usually contained in a single piece of wood. As their name suggests, they inhabit dry wood and can survive with very little access to water. Subterranean termites (Rhinotermitidae), in contrast, nest in soil or wood buried in soil, where they often form large colonies that extend above ground through an interconnected network of foraging tunnels. Colonies of the Formosan subterranean termite *Coptotermes formosanus*, for example, can contain millions of workers with foraging trails that stretch up to 100 meters.

While many termites are pests within their native range, the most specialized urban species are those that have become invasive [19]. Most invasive termites share three characteristics: they eat wood, they nest in wood, and they can generate secondary reproductives. Because cities use a vast amount of wood in buildings, they provide an abundance of food and nesting space. In addition, urban termites must be able to disperse to new cities and establish successful nests once they arrive. Since wood and lumber are global commodities, termites that nest in wood are regularly transported to new regions. Once they arrive, small propagules are more likely to succeed if they can produce secondary reproductives, which are workers, soldiers, or nymphs that can develop into mature reproductives when the primary reproductives are no longer present. Colonies may then generate numerous secondary reproductives to greatly increase reproductive output and to take advantage of the large food source construction lumber provides.

Although urban termites are almost always considered pests, termites have inspired at least one positive development in cities. The Eastgate

Centre in Harare, Zimbabwe was designed by architect Mick Pearce to mimic the passive cooling properties of local termite mounds [20]. The building incorporates two ventilation mechanisms inspired by early models of how termite mounds were thought to function. First, heat from the building's occupants and machinery is used to drive a thermosiphon that moves air from the building's lower floors to open stacks on the roof where the heat can escape. Second, as high winds blow across the open roof stacks, they create negative pressure in the stacks to help pull stagnant air out of the building. While later studies of termite mounds found that they do not function exactly as previous models suggested, the Eastgate Centre successfully reduced energy consumption by 10% and has inspired similar buildings, such as London's Portcullis House.

References

1. Savage, A. M., Hackett, B., Guénard, B., Youngsteadt, E. K., & Dunn, R. R. (2014). Fine-scale heterogeneity across Manhattan's urban habitat mosaic is associated with variation in ant composition and richness. *Insect Conservation and Diversity, 8*, 216–228.
2. Robinson, W. H. (2005). *Urban insects and arachnids: A handbook of urban entomology*. New York: Cambridge University Press.
3. Smith, A. E., & Secoy, D. M. (1975). Forerunners of pesticides in classical Greece and Rome. *Journal of Agricultural and Food Chemistry, 23*, 1050–1055.
4. Klotz, J. H., Hansen, L., Pospischil, R., & Rust, M. (2008). *Urban Ants of North America and Europe: Identification, Biology, and Management. Ithaca*. New York: Cornell University Press.
5. Rice, E. S., & Dunn, R. R. (2017). *Dr. Eleanor's book of common ants*. Chicago: University of Chicago Press.
6. Penick, C. A., Savage, A. M., & Dunn, R. R. (2015). Stable isotopes reveal links between human food inputs and urban ant diets. *Proceedings of the Royal Society B, 282*, 20142608.
7. Youngsteadt, E., Henderson, R. C., Savage, A. M., Ernst, A. F., Dunn, R. R., & Frank, S. D. (2014). Habitat and species identity, not diversity, predict the extent of refuse consumption by urban arthropods. *Global Change Biology, 21*, 1103–1115.
8. Diamond, S. E., Chick, L., Perez, A., Strickler, S. A., & Martin, R. A. (2017). Rapid evolution of ant thermal tolerance across an urban-rural temperature cline. *Biological Journal of the Linnean Society, 121*, 248–257.
9. Wetterer, J. K. (2010). Worldwide spread of the pharaoh ant, *Monomorium pharaonis* (Hymenoptera: Formicidae). *Myrmecological News, 13*, 115–129.
10. Penick, C. A., & Smith, A. A. (2015). The true odor of the odorous house ant. *American Entomologist, 61*, 85–87.
11. Wilson, J. S., & Carril, O. J. M. (2015). *The bees in your backyard: A guide to North America's bees*. Princeton: Princeton University Press.
12. Hall, D. M., Camilo, G. R., Tonietto, R. K., Ollerton, J., Ahrné, K., et al. (2017). The city as a refuge for insect pollinators. *Conservation Biology, 31*, 24–29.
13. Hernandez, J. L., Frankie, G. W., & Thorp, R. W. (2009). Ecology of urban bees: A review of current knowledge and directions for future study. *Cities and the Environment, 2*(3), 1–15.
14. Moore, L. J., & Kosut, M. (2013). *Buzz: Urban Beekeeping and the Power of the Bee* (p. 241). New York: NYU Press.
15. Penick, C. A., Crofton, C. A., Holden Appler, R., Frank, S. D., Dunn, R. R., & Tarpy, D. R. (2016). The contribution of human foods to honey bee diets in a mid-sized metropolis. *Journal of Urban Ecology, 2*, juw001.
16. Reed, H. C., & Vinson, S. (1979). Nesting ecology of paper wasps (*Polistes*) in a Texas urban area (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society, 52*, 673–689.
17. Hosaka, T., Sugimoto, K., & Numata, S. (2017). Effects of childhood experience with nature on tolerance of urban residents toward hornets and wild boars in Japan. *PLoS One, 12*, e0175243.
18. Rust, M. K., & Su, N.-Y. (2012). Managing social insects of urban importance. *Annual Review of Entomology, 57*, 355–375.
19. Evans, T. A., Forschler, B. T., & Grace, J. K. (2013). Biology of invasive termites: A worldwide review. *Annual Review of Entomology, 58*, 455–474.
20. Turner JS, Soar RC. (2008). Beyond biomimicry: What termites can tell us about realizing the living building. In *Proceedings of 1st International Conference on Industrialized, Integrated, Intelligent Construction, Loughborough,* Citeseer, pp. 221–37.