Records of rat control campaigns in a food market with the largest seafood trading volume worldwide

[1]Yasushi Kiyokawa, [1†]Ryoko Koizumi, [1]Ryoko Yamada, [3]Masayuki Hijikata, [2]Goro Kimura, [2]Kazuyuki D. Tanaka, [1]Yukari Takeuchi[2], and [2]Tsutomu Tanikawa

[1]Laboratory of Veterinary Ethology, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

[2]Technical Research Laboratory, Ikari Shodoku Corporation, 1-12-3 Akanehama, Narashino-shi, Chiba 275-0024, Japan

[3]Fukagawa Office, Ikari Shodoku Corporation, 4-2 Fuyuki, Koto-ku, Tokyo 135-0041, Japan

[†]Present address: Wildlife Damage Management Group, Central Region Agricultural Research Center, National Agricultural Food Research Organization, 2-1-18 Kannondaira, Tsukuba, Ibaraki 305-8666, Japan

Corresponding author: Yasushi Kiyokawa, Laboratory of Veterinary Ethology, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

E-mail: akiyo@mail.ecc.u-tokyo.ac.jp

Tel.: +81-3-5841-7577

Fax: +81-3-5841-8190

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Abstract

Brown rats (*Rattus norvegicus*) and roof rats (*Rattus rattus*) are among the most common mammals worldwide. Little is known about the effects of season on rat population size, which is important for understanding rat ecology and/or performing effective rat control campaigns. Tsukiji Market was a metropolitan central wholesale market in Tokyo and was located within 1 km from one of the biggest downtown areas. To control rats in the market, a pest management professional exclusively conducted annual campaigns at two fixed time points for many years. In addition, the pest management professional successfully confined all rats to the market and exterminated them when the market was closed and demolished. We analyzed these records to assess whether this rat population in Tokyo showed seasonal fluctuation and to provide information regarding rat management in a facility located in a downtown area. Multiple regression analyses revealed that trap success was affected by human activities (total trading volume and number of foreign tourists in Japan), but not by the month the campaign was performed. These results suggest that the rat population in this market did not show seasonal fluctuation. The results also suggest the importance of the effect of human activities on the ecological dynamics of rats in urban cities. We also described details of the campaigns performed as the market prepared to close to provide information regarding how to control rats in facilities in a downtown area.

Keywords

Norway rats, Black rats, Population size, Seasonal fluctuation, Absolute numbers

Introduction

Brown rats (*Rattus norvegicus*) and roof rats (*Rattus rattus*) are some of the most common mammals worldwide. Brown rats are thought to have originated in Southeast Asia and to have migrated to Northeast Asia approximately 173,700 years ago. Brown rats in Southeast Asia again spread to Middle Eastern Asia approximately 3,100 years ago and then reached Africa and Europe approximately 2,000 and 1,800 years ago, respectively (Zeng et al. 2018). Roof rats are thought to have had four ancestral populations that originally inhabited eastern and southern India, the western part of Indochina, the uplands of eastern Indochina, the Himalayan foothills, and the lower Mekong River catchment (Aplin et al. 2011). The first population migrated to Middle Eastern Asia approximately 15,000 years ago or earlier and then reached Europe. The second and fourth populations expanded their habitats, which covered Southeast Asia, Japan, and Micronesia, around 3,000 to 4,000 years ago. Then, both brown and black rats were shipped across the world from Europe during the Age of Exploration. Because of their high capacity to adapt to a wide variety of environments, rats adapted to coexistence with human populations and have lived in proximity to humans for thousands of years around the world. Consequently, rats are recognized as pests, rather than wild animals, in human society. For example, in the Toro Ruins in Japan, storehouses around 100 A.D. had a raised floor and were equipped with rat guards, which demonstrated that rats were already considered pests that exploit human resources. In addition, rats cause many zoonoses, including bubonic plague (Barnett 1948) and leptospirosis (Seijo et al. 2002). Even today, 17% and 5%–35% of brown rats in Tokyo, a metropolis with the largest number of residents globally (38,505,000 residents; Cox 2019), were reported to carry zoonotic leptospires (Koizumi et al. 2009) and helminths (Banzai et al. 2018), respectively.

The effect of season on rat population size has been a topic of research when studying rat ecology in urban cities. Given that trap success can be an index of population size (Emlen et al. 1949), changes in trap success have been measured. Some studies suggested the existence of seasonal fluctuation based on the observation that trap success increased and decreased around summer and winter, respectively (Traweger et al. 2006; Vadell et al. 2010). However, a greater number of attempts failed to find seasonality in trap success (Byers et al. 2019; Himsworth et al. 2014; Okutomi et al. 1999; Panti-May et al. 2016; Villafane et al. 2013; Yabe et al. 2016). Even in two studies that were conducted at the same town (a shanty town in Buenos Aires) during the same period (from September 2006 to August 2007), fluctuation was only observed in one study (Vadell et al. 2010; Villafane et al. 2013). One reason for this conflict may be that the surveys in these studies were performed within a relatively short period. Given that the duration ranged from 6 to 20 months, trap success at each time point was mostly measured once. It is possible that the natural variation of trap success obscured an existing fluctuation or produced a false fluctuation. An additional confounding factor may be that rats are thought to migrate between indoors and outdoors depending on season (Feng and Himsworth 2014; Himsworth et al. 2013). It is possible that trap success measured outside seasonally fluctuates when the number of migrating rats increases. Therefore, although this is important information for understanding rat ecology and/or performing effective rat control campaigns, there has been conflict among studies.

Tsukiji Market was established in 1935 as a metropolitan central wholesale market in Tokyo, Japan and had the largest seafood trading volume and turnover worldwide for many years (Table S1). Because the construction was planned during the reconstruction of Tokyo from the Great Kanto earthquake, the market had a large area (23 ha) but was located within 1 km of one of the biggest downtown areas. In addition to easy access, the market was not limited to professionals; people could enjoy the tuna auctions operated by large-sized wholesalers, and seafood and/or Japanese meals at restaurants. Consequently, Tsukiji Market was a major tourist spot in Tokyo (Endo 2016). To control rats in the market, a pest management professional exclusively conducted annual rat control campaigns at two fixed time points for many years. Therefore, analyzing these records allowed us to measure trap success at each time point multiple times. In addition, Tsukiji Market is suitable for analyzing rat population dynamics; the main part of the market was a one-story building with short walls, which prevented indoor and outdoor seasonal migration of rats. Furthermore, people in the market were tolerant of rats, and thus they made few culling attempts. Therefore, trap success would reflect the actual population size in the market. In addition to annual campaigns, the pest management professional conducted a campaign when Tsukiji Market was closed on 6 October 2018 and demolished because of relocation. Given that more than 400 shops had formed an outer market next to Tsukiji Market (Fig. 1A), no rats were allowed to evacuate Tsukiji Market during the demolition. The pest management professional successfully confined and exterminated all rats to the market and exterminated them. Therefore, the record of this campaign provides information that can contribute to effectively planning rat control campaigns during the demolition of facilities located in downtown areas.

There were two aims of the present study. First, we assessed whether a rat population in Tokyo showed seasonal fluctuation by analyzing trap success of the campaigns during 4 consecutive years. Second, we provided information regarding rat management in a facility located in a downtown area and described details of the campaign performed as the market prepared to close.

Materials and methods

Study site

Tsukiji Market was located in Tokyo, Japan (35°39′43′′N, 139°46′16′′E), and was surrounded by a broad river (southwest and southeast); a high-traffic, broad road (breadth, 33 m; northwest); and part of an outer market and another high-traffic, broad road (breadth, 31 m; northeast) (Fig. 1A). The market area was 230,836 m^2, including large-sized seafood, large-sized vegetable and fruit, mid-sized seafood, mid-sized vegetable and fruit wholesalers, refrigerators, processing plants, restaurants, parking, and associated trash collection areas (Fig. 1B). The mean respective annual temperatures and precipitation in Tokyo were 16.4 °C and 1781.5 mm (2015), 16.4 °C and 1779.0 mm (2016), 15.8 °C and 1430.0 mm (2017), and 16.8 °C and 1445.5 mm (2018). The weather data were obtained from Japan Meteorological Agency website (for more details, see Table S2).

The main part of the market was a one-story building with short walls. Partly because approximately 80 years had passed since construction, there were many gaps on the ground or between the ground and walls (Fig. S1). In addition, there were a lot of spaces underneath and/or behind refrigerators, fish tanks, wooden curb ramps, and/or duckboards. Empty Styrofoam boxes had been piled up for a long time in many wholesalers. Possible nests made of pieces of plastic bags and/or trash were found in these spaces during the demolition (Fig. S2). Rats in the market could eat food almost *ad libitum*. In the wholesalers, garbage and/or shavings of frozen fishes were always on the floor. Additionally, in the associated trash collection areas, garbage was not placed in sealed containers (Fig. S3). In addition, few people remained in the market after it closed early in the afternoon.

Rat control campaigns

Rat control campaigns in the market were exclusively conducted by a pest management professional (Ikari Shodoku Corporation) under a contract with the general incorporated association of the market and the Tokyo Metropolitan Government. All available records were provided by Ikari Shodoku Corporation. Unfortunately, the records of culling conducted during May 2016 and before 2015 were lost.

Annual campaigns consistent of three-night culling events conducted twice per year, during the Golden Week (May) and O-bon (August) holidays, from 2015–2018. For each three-night culling, the large-sized seafood, large-sized vegetable and fruit, mid-sized seafood, and mid-sized vegetable and fruit wholesalers; processing plants; and restaurants were divided into 6–15 subareas. Then, 4,000 glue traps (Chu Clean: 165 × 215 mm, Ikari Shodoku, Tokyo, Japan) and 40 live traps (230 × 140 × 100 mm: Tanaka Wire & Metal, Osaka, Japan) baited with a piece of fish sausage were placed in the afternoon on the first day (Fig. S4). Live traps were used for the places where no roof was available. Additionally, 70 kg of poison bait that contained 0.05% Warfarin (Neo Latte P, Ikari Shodoku) was mixed with the same amount of breadcrumbs, and approximately 250 g was placed on pans (Fig. S4). The locations of traps and poison bait were determined based on the information obtained from the market staff and upon inspection by the pest management professional. As a result, the locations were similar among three nights of a campaign and among the campaigns. Traps and poison bait were checked and replenished during the morning for 3 successive days. When a trap caught a rat, the trap was replaced with a new trap. Similarly, the poison bait was replenished when the amount decreased. The total number of rats trapped either by glue and live traps within a subarea was recorded in each subarea. The species of trapped rats were only visually determined during the two campaigns conducted in 2017 and was recorded if both brown rats and roof rats were trapped.

We defined the campaigns performed after 3 September as closure campaigns. From 1–3 September 2018, isolating walls were constructed to confine rats to the market (Fig. 1C). When we compared the four edges of the market, rats were predicted to evacuate less from the market through the southwest and southeast edges because they faced a broad river. It is unlikely that rats dove into the river and swam across it, although such behavior was reported in a specific experimental situation (Russell et al. 2005). The levees and/or broad open spaces further prevented rats from reaching the river (Fig. S5). Therefore, the isolating walls were erected along the remaining two edges. When there were already concrete block walls, holes in the walls were covered by perforated metal (Fig. S6). When new walls were constructed, sheet metal panels were used as much as possible (Fig. S6), but corrugated polycarbonate sheets were used as an alternative if necessary (Fig. S6). The gaps between the walls were carefully checked and filled by the pest management professional.

Closure campaigns were conducted from 5 September to 15 November 2018. The market was divided into five sections as follows: 1) large- and mid-sized vegetable wholesalers, 2) processing plants and restaurants, 3) parking, refrigerators, and associated trash collection areas, 4) large-sized seafood wholesalers, fish and shellfish tanks, and associated trash collection areas, and 5) mid-sized seafood wholesalers (Fig. 1D). In addition, the area within 1 m of the market edges was defined as the peripheral area.

On the morning of 5 September, 400 live traps (Tanaka Wire & Metal) baited with a piece of salami were placed in the peripheral area with a 10-m space between each trap to further prevent rats from evacuating the market. The traps were checked every 3 or 4 days. When the trap caught a rat, it was replaced with a new trap.

Two-night culling events were conducted on two 3-day weekends: 15–17 and 22–24 September.

In the first campaign, 7,000 glue traps (Chu Clean), 50 live traps (Tanaka Wire & Metal) baited with a piece of fish sausage, and 30 kg of poison bait that contained 0.05% Warfarin (Neo Latte P) and mixed with the same amount of breadcrumbs were placed throughout the five sections in the afternoon on the first day. The second campaign was conducted in a similar manner, except 8,000 glue traps were used. For both campaigns, traps and poison bait were checked and replenished during the morning of the following 2 days.

A large-scale campaign was conducted from 11 October–15 November, because the businesses were moved out of the market by 10 October. The campaign was divided into two halves (11–18 October and 18 October–15th November). In the first half, 21,000 glue traps (Chu Clean) and 50 live traps (Tanaka Wire & Metal) baited with a piece of fish sausage, and 170 kg of poison bait containing 0.05% Warfarin (Neo Latte P) were doubled with breadcrumbs and placed throughout the five sections on the morning of 11 October. Additionally, 20 kg of poison bait containing 0.75% Coumatetralyl (Endox: Bayer Crop Science, Tokyo, Japan) was diluted 30 times with breadcrumbs and placed in the 1) large- and mid-sized vegetable wholesaler section because the presence of roof rats was suspected. Then, traps and poison bait were checked and replenished as necessary during the morning in the following 7 successive days. In addition, fresh carcasses on the ground were collected. In the second half of the campaign, 24,800 glue traps (Chu Clean) and 40 live traps (Tanaka Wire & Metal) baited with a piece of fish sausage, and 150 kg of poison bait that contained 0.05% Warfarin (Neo Latte P) and mixed with the same amount of breadcrumbs were placed throughout the five sections on the morning of 18 October. Then, traps and poison bait were checked and replenished, and fresh carcasses on the ground were collected every 3–5 days.

In all campaigns, trap success was calculated by dividing (number of rats caught by glue or live traps × 100) by (number of glue and live traps × number of nights the traps were placed) (Panti-May et al. 2016; Traweger et al. 2006). Carcasses on the ground were not incorporated into the calculation.

Statistical analyses

The data were expressed as means ± standard error of the mean, and significance was set at *P*

< 0.05 for all statistical tests.

Multiple linear regression was used to clarify whether month (May or August) was associated with trap success in annual campaigns and to elucidate the factors associated with trap successes. The normality of trap success was first checked by Shapiro–Wilk test. To assess the effects of month, month was used as an explanatory variable. To search additional explanatory variables, we chose the following factors that potentially affected trap success: year (2015, 2016, 2017, and 2018), day of culling (1st, 2nd, and 3rd), number of foreign tourists in Japan, total trading volume, total precipitation, average daily temperature, average daily high temperature, average daily low temperature, highest temperature, lowest temperature, average daily humidity, lowest humidity, and sunlight hours. The number of foreign tourists in Japan was included, because the amount of waste in the market, especially from restaurants, changes depending on the number of visitors. Given that the market was a popular tourist spot in Tokyo, it is reasonable to assume that the number of tourists visiting the market changed along with the number of tourists in Japan. The number of foreign tourists in Japan was obtained from the Japan National Tourism Organization website (Table S3). The Japan National Tourism Organization calculates this by subtracting the number of visitor arrivals to Japan who answered their purpose as “business” or “other” from the total number of visitor arrivals to Japan. The total number of visitor arrivals to Japan were provided by the Ministry of Justice and calculated based on the number of travelers of foreign nationality entering Japan. Those figures exclude crew members and permanent residents that have Japan as their primary place of residence, and include travelers entering Japan for the purpose of transit, foreigners entering or re-entering Japan, such as expatriates and their families, and international students. Additionally, each instance of entry into the country/area is counted as one person. For example, if the same person visits Japan once in January and then again in September, they are counted as two people. Total trading volume of the market was included because it could affect the amount of garbage in the market. The data were obtained from the Tokyo Metropolitan Government website (Table S1). Weather data were obtained from the Japan Meteorological Agency website (Table S2). The data were measured at a park in Tokyo located approximately 3.5 km away from the market (35°41′30″N, 139°45′00″E, 25.2 m above sea level) through the Automated Meteorological Data Acquisition System, which is operated by the Japan Meteorological Agency. Given that population size is mostly determined by mortality in neonates and juveniles rather than adults (Calhoun 1962; Vadell et al. 2010), the summarized/averaged/highest/lowest data from March to May and from June to August were used to analyze trap success in May and August, respectively. These factors were standardized and individually assessed by simple linear regression. In addition to month, only factors that were associated with trap success with a $P < 0.10$ were selected as explanatory variables in the multiple linear regression models. However, the factors that significantly correlated with each other, as revealed by Spearman's rank correlation test, were considered in separate competing models. Then, we established possible models and compared Akaike's information criterion (AIC). The presence of multicollinearity was checked by calculating variance inflation factor (VIF) or generalized variance inflation factor (GVIF). Regression analyses were conducted using R version 3.6.1.

For the closure campaign, the effectiveness of live traps placed in the peripheral area was assessed by comparing trap success between the five sections and in the peripheral area during the market opening (3–25 September 2018) and after the market closed (11 October to 15 November). The averaged trap success during the periods were assessed by a Student's *t*-test. In addition, the biased distribution of rats within the market was clarified by comparing trap success among the five sections from 12–17 October, because detailed records were only available for this period (Table S4). The average trap successes in each section were assessed by a one-way ANOVA followed by Tukey–Kramer HSD post hoc test.

Results

Factors that influenced trap success in annual campaigns

The annual campaign records are summarized in Table 1. Trap successes in annual campaigns were normally distributed ($P = 0.29$). Simple linear regression analyses revealed that year ($P < 0.05$), number of foreign tourists in Japan ($P < 0.01$), total trading volume ($P < 0.01$), average daily humidity (*P*

< 0.1), and lowest humidity ($P < 0.05$) were associated with trap success. In contrast, day of culling (*P*s > 0.1), total precipitation ($P = 0.41$), average daily temperature ($P = 0.14$), average daily high temperature ($P = 0.12$), average daily low temperature ($P = 0.17$), highest temperature ($P = 0.47$), lowest temperature ($P = 0.13$), and sunlight hours ($P = 0.89$) were less associated with trap success. Therefore, the factors associated with trap success were used as explanatory variables in addition to month. Spearman's rank correlation test revealed that month, average daily humidity, and lowest humidity were correlated with each other (Table S5). Similarly, year, number of foreign tourists in Japan, and total trading volume were correlated with each other (Table S5). Therefore, we established nine multiple linear regression models using month, average daily humidity, or lowest humidity along with year, number of foreign tourists in Japan, or total trading volume as explanatory variables. When we compared these models, trap success was most effectively explained in the model using total trading volume and lowest humidity as explanatory variables (Table 2). We found that trap success decreased when total trading volume increased (Table 2). However, because month was not used as an explanatory variable, we could not specify the role of month in trap success in this model. Therefore, we further checked the details of the other models. We found that month did not affect trap success in any models when selected as an explanatory variable (Table 2). The VIF/GVIF of the variables were highest (1.77) in the best model.

Characteristics of trapped rats in annual campaigns

We could determine the number of roof rats recorded in the campaigns conducted in May 2017, because brown rats and roof rats were caught in different subareas; of the 409 trapped rats, 400 (98.0%) were brown rats and nine (2.0%) were roof rats. Of the nine roof rats, one and eight were trapped at mid-sized vegetable wholesalers and restaurants, respectively. However, in the campaigns conducted in August 2017, all roof rats were trapped in areas where brown rats were simultaneously caught. Accordingly, of the 589 trapped rats, 556–586 (94.4%–99.5%) could have been brown rats, whereas 3–33 (0.5%–5.6%) could have been roof rats. Of the 3–33 roof rats, 1–4, 1–8, and 1–18 were trapped at mid-sized vegetable wholesalers, restaurants, and processing plants, respectively.

Details of trapped rats during the closure campaign

The closure campaign records are summarized in Table 3. A total of 1,724 rats were trapped. Of these rats, 1,490 (86.4%) and 88 (5.1%) rats were caught in the five sections and the peripheral area, respectively, whereas 146 (8.5%) rats were found as carcasses on the ground.

In closure campaign, during the market opening, trap success was higher in the five sections than the peripheral area ($t_8 = -3.46$, $P < 0.01$). However, after the market closed, trap success was similar between these places. During 12–17 October, trap success differed among the five market sections ($F(4,25) = 3.45$, $P < 0.05$) (Fig. S7). A post hoc test revealed that trap success in 5) mid-sized seafood wholesalers was higher than in 1) large- and mid-sized vegetable wholesalers ($P < 0.05$) and 3) parking, seafood freezing warehouses, and associated trash collection areas ($P < 0.05$). Trap success was moderate in 2) processing plants and restaurants and 4) large-sized seafood wholesalers, fish and shellfish tanks, and associated trash collection areas.

Discussion

In the present study, we analyzed the records of rat control campaigns conducted at a food market that had the largest seafood volume and turnover worldwide. Multiple regression analyses of the records during 4 consecutive years revealed that trap success was not affected by month. These results suggest that the rat population in this market did not show seasonal fluctuation. In contrast, an increase in total trading volume in the preceding 3 months was found to have negative effects on trap success. In addition, the number of foreign tourists in Japan was also suggested to affect trap success in the other models. These results indicate that human activities had prominent effects on the population in the market. We also described details of the campaigns performed when the market closed. Given that the closure campaign successfully confined and exterminated all rats, this information could be helpful to those who are planning rodent management strategies during the demolition of a facility in downtown areas.

Based on the present findings, we suggest that this rat population did not show seasonal fluctuation. In all models tested by multiple regression analyses, month was not the significant explanatory variable for trap success. In contrast, human activities were found to affect trap success. Specifically, the total trading volume was found to have negative effects on trap success. In addition, the models using the number of foreign tourists in Japan as an explanatory variable showed comparable AIC values with the best model. These models indicated that trap success increases when the number of foreign tourists in Japan increases. Furthermore, total trading volume and number of foreign tourists in Japan were significantly correlated. Therefore, these factors might cooperatively affect population size. The substantial contribution of human activities in determining rat population size may explain the conflicting information regarding seasonal fluctuation in populations in previous studies. For example, when surveys were performed at places where human activities showed clear seasonality, the rat populations seemed to seasonally fluctuate. In contrast, no seasonal fluctuation was observed when human activities were stable throughout a year. Therefore, human activities should be taken into consideration when examining rat population dynamics, as we included total trading volume and number of foreign tourists in Japan in the present study. However, in the present study, the records of the annual campaign conducted during May 2016 were not available. In addition, the interval between the two time points (May and August) was relatively short. Therefore, further research is needed to draw a more robust conclusion.

In contrast to our intuition, trap success decreased when total trading volume increased. One reason for this relationship might be that the frequency of floor washing increased along with total trading volume. As revealed by the comparison of trap success among the five sections, rats mainly infested the mid-sized seafood wholesalers. When the market was open, mid-sized seafood wholesalers frequently washed the floor with filtered seawater provided by the market, which helped improve hygiene by preventing the prevalence of insects (flies) and leptospires (Trueba et al. 2004). Therefore, it is possible that increased trading volume increased the frequency of floor washing. As a result, garbage and/or shavings of frozen fishes were on the floor for less time, which deprived most rats of available food. Given that rats in the mid-sized seafood wholesalers nested underneath and/or behind of refrigerators, fish tanks, wooden curb ramps, and/or duckboards, frequent washing might also limit spaces for nesting. Consequently, the population size decreased.

Based on the present and previous findings, it is possible that a rat population dynamically changes, even if the size is stable throughout a year. Although we had no information regarding population breakdown, it was frequently observed that the proportions of pregnant and lactating females changed without consistent seasonality. For example, some populations showed a unimodal peak, whereas bimodal peaks were observed in the other populations. The peaks varied among seasons in different populations (Butler and Whelan 1994; Davis 1953; Davis and Hall 1951; Himsworth et al. 2014). Similarly, a 3-year survey at the same place in Yokohama, Japan, a prefecture next to Tokyo Metropolis, found that a peak in juvenile recruitment was not consistent among 3 years; i.e., peaks were observed in October 2014, January 2015, and May and September 2016 (Yabe et al. 2016). It is well known that reproduction occurs throughout the year (Feng and Himsworth 2014). Furthermore, it was reported that females and their neonates were more vulnerable to stress caused by high density than males (Calhoun 1962). Based on these findings, it is possible that the population does not change its size but varies its breakdown. Specifically, the proportion of females and juveniles is low when the population size is close to carrying capacity of the habitat. When the population size is decreased by certain events (e.g., culling, changes in garbage collecting system, closure of neighboring shops), the mortality rate of females and neonates immediately decreases. Therefore, females and neonates compensated for the decreased population numbers, which resulted in a high proportion of females and juveniles. Future longitudinal and comprehensive studies are necessary to assess this possibility.

The records of two annual campaigns conducted in 2017 demonstrated that brown rats were predominant in the market. This seems not to be an artefact caused by the trapping methods in this study. The pest management professionals also expected this result based on their inspections, although the results of inspections were not officially recorded. The predominance of brown rats greatly contrasts the situation in most cities in Japan, where roof rats were reported to be predominant (Harunari et al. 2009; Yabe 1997a; Yabe 1997b; Yabe et al. 2000). Indeed, when rats were trapped in 27 buildings in three large cities in Japan, all of the 1,720 trapped rats were roof rats (Tanikawa et al. 2007). One reason for this difference could be that most parts of the market were one-story buildings. In addition, there was a lot of food on the ground level, as opposed to buildings where food resources for rats are usually available at the top (such as restaurants) and/or underground (such as food shops) in Japan (Okutomi et al. 1999). These environments forced brown rats and roof rats to live in the same area. When these two rats coexist, brown rats usually exclude roof rats, because brown rats are larger and more aggressive than roof rats (Barnett 1958; Worth 1950); this could explain why brown rats outnumbered roof rats in the market.

The closure campaigns at Tsukiji Market successfully confined and exterminated all rats. The following factors may have contributed to the success. First, isolating walls were constructed when the market opened. The findings that trap success in the peripheral area became comparable to that in the five sections after the market closed suggested that rats started to roam all over the market when availability of foods in the five sections was reduced. Therefore, it is highly possible that rats spread to neighboring areas if there were no walls. In Tsukiji Market, the broadness of the gates and the presence of gatekeepers at the end of the gate further helped to confine rats inside the market. These features prevented rats from passing through the opened gates. Second, wastewater in the market was pumped into the sewage system. Although rats migrate through the sewage systems in urban cities (de Masi et al. 2009; Langton et al. 2001), it is difficult for rats to pass through the pump. This was confirmed by the fact that trap success in sewers around the market decreased after the market closed, even though it was stable in the previous year. Specifically, trap success in August, September, October, and November was 1.9780, 2.5581, 2.5108, and 1.3678 in 2018, respectively, compared with 1.2658, 2.3810, 3.0864, and 2.4691 in 2017, respectively (calculated based on the data obtained from the local government by requesting this information). If wastewater had directly flowed into the sewage systems, barriers should have been placed in the drainage pipes. Third, rodenticide was replenished until the end of campaign. In the campaign, rodenticide was mixed with breadcrumbs. Therefore, the less available foods in the market became, the more attractive breadcrumbs with rodenticide became. This might have supported the extermination of a small number of the remaining rats around the end of the campaign when glue and live traps were not effective.

In Tsukiji Market, the closure campaign was successfully implemented by the pest management professional without additional contributions of other organizations. However, this does not necessarily deny the importance of the Boston Model (Colvin and Jackson 1999). When a new highway was constructed in Boston, Massachusetts (USA), a comprehensive rodent control program during 1990 resulted in great success. This led to the formation of the Boston Model for rodent management. In this model, the following four components are suggested to be important factors for success. The primary component is the management function that is performed by personnel (a biologist) skilled in technical aspects of rodent control that also have contract management, public relations, engineering, scheduling, and computer-based mapping, and data management skills. The second component is municipal functions, which are performed by the Inspectional Services Department, Code Enforcement Police, Water and Sewer Commission, and Public Works Department. The third component involves pest control contractors who perform poison baiting, trapping, and monitoring. The fourth component is public participation, which is championed by community leaders and organizations. These various components were integrated to maximize the skills and participation of each group within the program. One obvious reason why the closure campaign lacked the collaboration of other organizations but was still successful is that Tsukiji Market (0.23 km^2) is much smaller than the targeted area in Boston (18 km^2). An additional reason may be that the pest management professional was sufficiently able to perform the campaign alone. The primary and third components were included by the company. The second and fourth components were not necessary, because the campaign was performed within one facility. The existence of pumps between the market and the sewage system also decreased the necessity of the second component. However, if the target area included public space and residential areas, the second and fourth components might be required. In addition, if the campaign was performed by multiple companies, the first component should have been included. Taken together, although the four components are important for implementing campaigns, it is not necessary to incorporate all components in all scenarios.

In conclusion, we suggest that the rat population in Tsukiji Market did not show seasonal fluctuation. In addition, human activities were found to have a greater effect on population size than weather. However, it is possible that weather significantly affects population size when the population is located in different climatic zones where winter weather is more severe than in Tokyo. Indeed, although it was not statistically assessed, trap success at pig farms in County Kildare, Ireland seemed to decrease during winter (Butler and Whelan 1994). Similarly, gonadal activities of rats that inhabited outdoor farms were found to be suppressed in both sexes during winter in Harbin, China (Wang et al. 2011). In addition, the existence and intensity of seasonal fluctuation in human activities varies by location. Although the number of foreign tourists in Japan and total trading volume did not correlate with month in Tsukiji Market, human activities can show seasonal fluctuation in the other places. Therefore, even within the same climatic zone or within the same city, it is possible that some populations show seasonal fluctuation but not others. When we think about a population from the perspective of pest management, it is important to clarify whether the target population seasonally fluctuates. This can be clarified by conducting a census prior to performing the control campaign. However, from an ecological perspective, it is important to clarify why the population shows seasonal fluctuation. Future ecological studies will become more comprehensive if they include both weather data and human activities as candidate explanatory variables of rat population size.

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Table 1. Annual campaign records

Trapped rats	Trap success	Date
47a	1.1634	3 May 2015
98a	2.4257	4 May 2015
72a	1.7822	5 May 2015
84b	2.0792	14 August 2015
140b	3.4653	15 August 2015
123b	3.0446	16 August 2015
248c	6.1386	14 August 2016
225c	5.5693	15 August 2016
119c	2.9455	16 August 2016
114d	2.8218	3 May 2017
135d	3.3416	4 May 2017
160d	3.9604	5 May 2017
114e	2.8218	13 August 2017
224e	5.5446	14 August 2017
251e	6.2129	15 August 2017
171f	4.2327	4 May 2018
278f	6.8812	5 May 2018
250f	6.1881	6 May 2018
160g	3.9604	16 August 2018
314g	7.7723	17 August 2018
265g	6.5594	18 August 2018

4,000 glue traps, 40 live traps, and 70 kg rodenticide were placed from:
a: 2–5 May 2015
b: 13–16 Aug. 2015
c: 13–16 Aug. 2016
d: 2–5 May 2017
e: 12–15 Aug. 2017
f: 3–6 May 2018
g: 15–18 Aug. 2018

Table 2. Comparison of candidate models to predict trap success in annual campaigns

Models	df	AIC	Adjusted R^2	Estimate	Standard Error	*t* value	*P* value
[1] Lowest humidity + Total trading volume	18	–14.4	0.56				
Intercept				-1.16×10^{-9}	0.14	0	1
Total trading volume				–0.84	0.20	–4.27	0.00046
Lowest humidity				–0.11	0.20	–0.54	0.60
[2] Month + Total trading volume	18	–14.1	0.55				
Intercept				0.023	0.23	0.098	0.92
Total trading volume				–0.78	0.16	–4.82	0.00014
Month (August)				–0.040	0.32	–0.13	0.90
[3] Average daily humidity + Total trading volume	18	–14.1	0.55				
Intercept				-9.43×10^{-10}	0.15	0	1
Total trading volume				–0.78	0.17	–4.51	0.00027
Average daily humidity				-8.33×10^{-3}	0.17	–0.048	0.96
[4] Average daily humidity + Number of foreign tourists in Japan	18	–12.8	0.52				
Intercept				-1.27×10^{-8}	0.15	0	1
Number of foreign tourists in Japan				0.67	0.16	4.24	0.00049
Average daily humidity				0.22	0.16	1.38	0.18
[5] Month + Number of foreign tourists in Japan	18	–12.7	0.52				
Intercept				–0.24	0.23	–1.04	0.31
Number of foreign tourists in Japan				0.7	0.16	4.54	0.00026
Month (August)				0.42	0.31	1.37	0.19
[6] Lowest humidity + Number of foreign tourists in Japan	18	–11.7	0.50				
Intercept				-9.26×10^{-9}	0.15	0	1
Number of foreign tourists in Japan				0.65	0.18	3.72	0.0016
Lowest humidity				0.17	0.18	0.98	0.34
[7] Average daily humidity + Year	16	–11.6	0.53				
Intercept				–0.92	0.28	-3.23	0.0052
Year 2016				1.05	0.52	2.03	0.060
Year 2017				0.88	0.40	2.22	0.041
Year 2018				1.81	0.40	4.54	0.00033
Average daily humidity				0.26	0.16	1.61	0.13
[8] Month + Year	16	–11.5	0.53				
Intercept				–1.26	0.32	-3.89	0.0013
Year 2016				1.10	0.51	2.14	0.048
Year 2017				0.94	0.40	2.38	0.030
Year 2018				1.90	0.40	4.80	0.00020
Month (August)				0.51	0.32	1.60	0.14
[9] Lowest humidity + Year	16	–10.9	0.52				
Intercept				–0.94	0.29	-3.27	0.0048
Year 2016				1.35	0.49	2.75	0.014
Year 2017				0.94	0.4	2.35	0.032
Year 2018				1.68	0.43	3.87	0.0014
Lowest humidity				0.24	0.17	1.41	0.18

Table 3. Closure campaign records

Five sections			Date	Peripheral area	
Carcasses	Trapped rats	Trap success		Trapped rats	Trap success
			During market opening		
			8 September 2018	5a	0.4167
			11 September 2018	5a	0.4167
			14 September 2018	4a	0.3333
	88b	1.2482	16 September 2018		
	129b	1.8298	17 September 2018	4a	0.3333
			21 September 2018	8a	0.5000
	44c	0.5466	23 September 2018		
	74c	0.9193	24 September 2018		
			25 September 2018	4a	0.2500
			29 September 2018	7a	0.4375
			3 October 2018	6a	0.3750
			After market closure		
			7 October 2018	0a	0.0000
			11 October 2018	17a	0.4722
	403d	1.9145	12 October 2018		
	173d	0.8219	13 October 2018		
	83d	0.3943	14 October 2018		
5d	67d	0.3183	15 October 2018	7a	0.4375
10d	47d	0.2233	16 October 2018		
56d	140d	0.6651	17 October 2018		
34d	25d	0.1188	18 October 2018		
8e	63e	0.0507	23 October 2018	9a	0.2813
15e	79e	0.0795	27 October 2018	8a	0.5000
7e	24e	0.0242	31 October 2018	2a	0.1250
1e	11e	0.0089	5 November 2018	0a	0.0000
5e	21e	0.0282	8 November 2018	2a	0.1667
1e	4e	0.0040	12 November 2018	0a	0.0000
4e	15e	0.0201	15 November 2018	0a	0.0000

a: 400 live traps were placed from 5 Sep.–15 Nov. 2018

b: 7,000 glue traps, 50 live traps, and 30 kg rodenticide were placed from 15–17 Sep. 2018

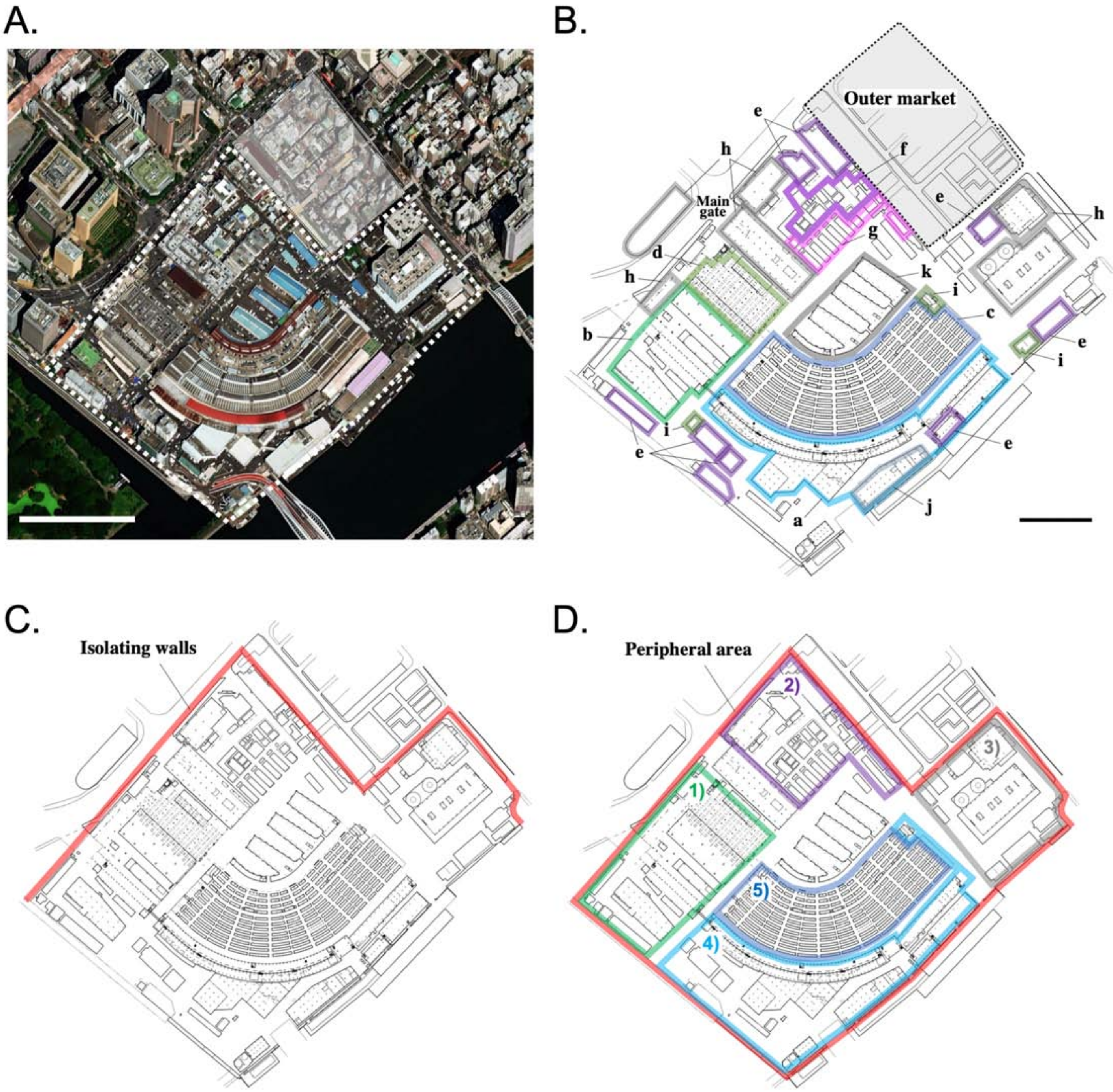
c: 8,000 glue traps, 50 live traps, and 30 kg rodenticide were placed from 22–24 Sep. 2018

d: 21,000 glue traps, 50 live traps, and 190 kg rodenticide were placed from 11–18 Oct. 2018

e: 24,800 glue traps, 40 live traps, and 150 kg rodenticide were placed from 18 Oct.–15 Nov. 2018

Figure captions

Fig. 1. Map and schematic diagram of Tsukiji Market. (A) A satellite picture of the market adapted from Yahoo! maps. The market is indicated with the white dotted line. The shaded area indicates the outer market. The horizontal bar indicates 200 m. (B) The location of facilities in the market. a. Large-sized seafood wholesaler, b. large-sized vegetable and fruit wholesaler, c. mid-sized seafood wholesaler, d. mid-sized vegetable and fruit wholesaler, e. refrigerator, f. processing plants, g. restaurant, h. parking, i. associated trash collection areas, j. fish and shellfish tanks, k. loading dock. The horizontal bar indicates 100 m. (C) Location of isolating walls. (D) Location of the five sections and peripheral area.



A.
B.
Outer market
e
h
f
Main gate
g
d
k
i
c
b
j
a
C.
Isolating walls
D.
Peripheral area
1)
2)
3)
4)
5)

Table S1. General market information

	Winter	Spring	Summer	Autumn	Year
Number of mid-sized seafood / vegetable wholesalers					
2014					651 / 103
2015					606 / 102
2016					558 / 97
2017					538 / 97
2018					488 / 96 a
Trading volume (kg)					
Seafood					
2014				116,582,069	452,414,872
2015	110,300,386	114,315,439	104,766,890	108,733,314	436,273,849
2016	104,889,490	107,213,531	97,046,288	103,286,045	409,866,591
2017	98,345,967	101,148,507	91,749,665	95,667,272	385,004,700
2018	93,193,319	96,799,206	86,165,116		266,929,454*
Vegetable					
2014				75,639,368	292,462,292
2015	70,803,964	63,778,168	66,493,552	71,104,079	271,656,773
2016	69,104,177	62,806,766	64,635,757	66,710,989	262,014,752
2017	68,635,420	64,631,619	64,843,206	66,409,416	262,215,259
2018	59,166,933	59,035,321	61,147,671		175,318,096*
Total					
2014				192,221,437	744,877,164
2015	181,104,350	178,093,607	171,260,442	179,837,393	707,930,622
2016	173,993,667	170,020,297	161,682,045	169,997,034	671,881,343
2017	166,981,387	165,780,126	156,592,871	162,076,688	647,219,959
2018	152,360,252	155,834,527	147,312,787		442,247,550*
Turnover (Yen)					
Seafood					
2014				111,104,423,763	435,022,633,269
2015	118,073,516,219	108,130,065,881	104,832,909,904	110,751,912,146	440,144,625,561
2016	115,489,838,523	104,096,494,000	99,596,000,138	110,332,391,034	429,211,681,478
2017	115,296,656,075	105,839,484,987	99,850,880,963	107,660,258,282	427,734,947,612
2018	111,043,795,027	103,761,247,300	97,729,868,547		293,265,084,466*
Vegetable					
2014				20,829,404,766	86,361,546,495
2015	22,851,268,549	22,446,279,814	22,581,968,331	21,376,696,934	88,955,890,450
2016	22,678,290,553	22,333,924,076	21,560,023,702	23,498,663,204	90,862,192,223
2017	23,692,932,941	21,860,286,065	21,261,562,553	20,799,265,315	87,963,339,487
2018	24,345,053,368	20,295,267,300	21,720,678,058		64,005,785,982*
Total					
2014				131,933,828,529	521,384,179,764
2015	140,924,784,768	130,576,345,695	127,414,878,235	132,128,609,080	529,100,516,011
2016	138,168,129,076	126,430,418,076	121,156,023,840	133,831,054,238	520,073,873,701
2017	138,989,589,016	127,699,771,052	121,112,443,516	128,459,523,597	515,698,287,099
2018	135,388,848,395	124,056,514,600	119,450,546,605		357,270,870,448*

Winter: Dec. previous year to Feb.

Spring: Mar. to May

Summer: Jun. to Aug.

Autumn: Sep. to Nov.

Year: Jan. to Dec.

*: Summarised through the end of Sep.

a: Numbers obtained in Apr. 2019

Data obtained from the Tokyo Metropolitan Government website

Table S2. Tokyo weather data

	Winter	Spring	Summer	Autumn	Year
Total precipitation					
2014				638.5	1808.0
2015	216.5	311.0	533.5	700.0	1781.5
2016	224.5	360.5	670.0	522.5	1779.0
2017	125.5	256.5	329.0	788.0	1430.0
2018	83.5	494.5	349.0		1445.5
Temperature					
Daily average					
2014				18.8	16.6
2015	6.1	15.3	25.0	18.3	16.4
2016	7.5	15.2	25.0	18.2	16.4
2017	7.2	14.4	25.2	17.2	15.8
2018	5.6	16.1	26.3		16.8
Daily high average					
2014				22.4	20.5
2015	10.6	20.4	29.0	22.3	20.8
2016	12.1	20.1	29.2	21.9	20.9
2017	12.2	19.5	29.5	21.2	20.4
2018	10.2	21.2	30.6		21.2
Daily low average					
2014				15.8	13.3
2015	2.2	10.8	21.9	15.1	12.8
2016	3.6	11.0	21.7	15.1	12.7
2017	2.9	10.1	22.0	13.9	12.1
2018	1.5	11.4	22.9		13.0
Highest					
2014				31.6	36.1
2015	19.2	32.2	37.7	31.5	37.7
2016	24.1	30.9	37.7	33.0	37.7
2017	20.6	30.9	37.1	33.3	37.1
2018	16.0	29.0	39.0		39.0
Lowest					
2014				6.9	-1.3
2015	-2.4	-0.4	13.4	3.9	-2.4
2016	-2.6	1.1	14.2	0.3	-2.6
2017	-2.3	0.0	14.8	3.2	-2.3
2018	-4.0	1.7	14.2		-4.0
Humidity					
Daily average					
2014				66.0	61.9
2015	55.3	63.3	77.7	73.0	67.5
2016	56.0	64.7	77.7	76.3	68.8
2017	53.7	66.0	78.0	76.0	68.2
2018	55.3	67.3	78.0		69.9
Lowest					
2014				20	8
2015	12	12	22	17	12
2016	11	9	17	29	9
2017	15	13	21	27	13
2018	14	16	28		14
Sunlight hours					
2014				415.6	2104.0
2015	534.1	584.3	456.7	414.7	1966.6
2016	523.6	516.0	439.3	331.1	1841.7
2017	614.1	606.0	431.6	381.8	2050.9
2018	584.5	599.1	607.7		2112.2

Winter: Dec. previous year to Feb

Spring: Mar. to May

Summer: Jun. to Aug.

Autumn: Sep. to Nov.

Year: Jan. to Dec.

Data obtained from the Japan Meteorological Agency website

Table S3. Numbers of foreign tourists in Japan

	Winter	Spring	Summer	Autumn	Year
2014				2,819,994	10,880,604
2015	3,260,068	4,176,963	4,696,132	4,310,776	16,969,126
2016	4,849,849	5,192,242	5,645,486	5,096,741	21,049,676
2017	5,662,792	6,219,646	6,751,971	6,356,179	25,441,593
2018	6,767,817	7,278,788	7,314,134		27,766,112

Winter: Dec. previous year to Feb.

Spring: Mar. to May

Summer: Jun. to Aug.

Autumn: Sep. to Nov.

Year: Jan. to Dec.

Data obtained from the Japan National Tourism Organization website

Table S4. Detailed extermination records

Large- and mid-sized vegetable wholesalers		Processing plants, restaurants		Parking, seafood freezing warehouses, associated trash collection area		Large-sized seafood wholesalers, fish and shellfish tanks, associated trash collection area		Mid-sized seafood wholesalers		Date
Trapped rats	Trap success	Trapped rats	Trap success	Trapped rats	Trap success	Trapped rats	Trap success	Trapped rats	Trap success	
30a	0.6000	35b	0.6972	1c	0.0990	47d	1.5563	290e	4.1429	12 Octorber 2018
5a	0.1000	21b	0.4183	5c	0.4950	34d	1.1258	108e	1.5429	13 Octorber 2018
6a	0.1200	13b	0.2590	2c	0.1980	4d	0.1325	58e	0.8286	14 Octorber 2018
4a	0.0800	8b	0.1594	0c	0.0000	11d	0.3642	44e	0.6286	15 Octorber 2018
8a	0.1600	4b	0.0797	1c	0.0990	6d	0.1987	28e	0.4000	16 Octorber 2018
16a	0.3200	30b	0.5976	2c	0.1980	9d	0.2980	83e	1.1857	17 Octorber 2018

a: 5,000 glue traps and 40 kg rodenticide were placed from 11-17th Oct. 2018

b: 5,000 glue traps, 20 live traps and 28.75 kg rodenticide were placed from 11-17 Oct. 2018

c: 1,000 glue traps, 10 live traps and 12.5 kg rodenticide were placed from 11-17 Oct. 2018

d: 3,000 glue traps, 20 live traps and 33.75 kg rodenticide were placed from 11-17 Oct. 2018

e: 7,000 glue traps and 75 kg rodenticide were placed from 11-17 Oct. 2018

Fig. S1. Pictures of gaps on the ground or between the ground and walls.

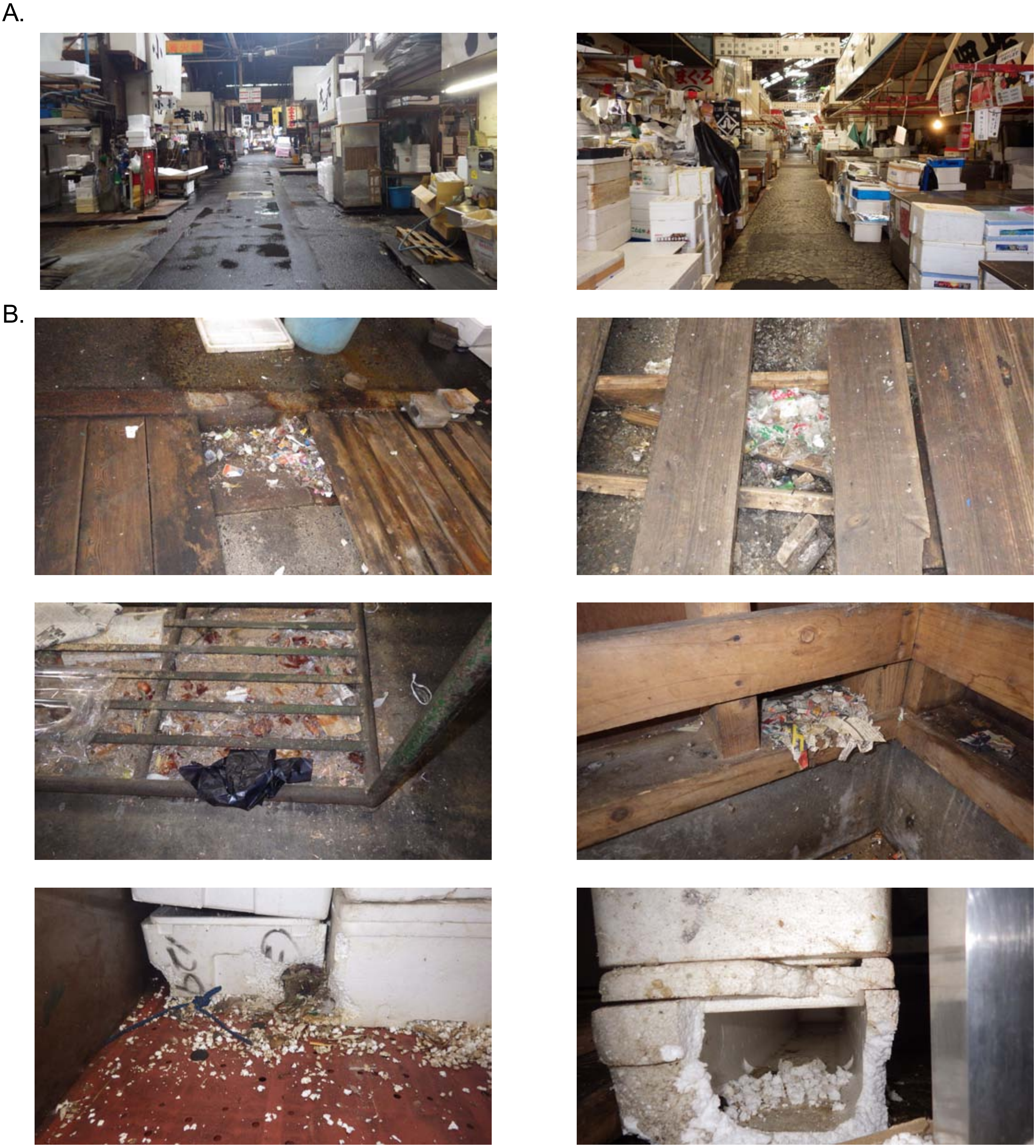


Fig. S2. Pictures in the market. (A) Mid-sized seafood wholesaler. (B) Possible nests made of pieces of plastic bags and/or trash found in spaces underneath and/or behind of refrigerators, fish tanks, wooden curb ramps, and/or duckboards. Possible nests were also found in empty styrofoam boxes that had been piled up for a long time.

Fig. S3. Pictures of garbage in the associated trash collection areas. Garbage was not placed in the sealed containers.

Fig. S4. Pictures of glue and live traps and rodenticides placed during the campaigns.

Fig. S5. Pictures of levees and/or broad open spaces between the market and river.

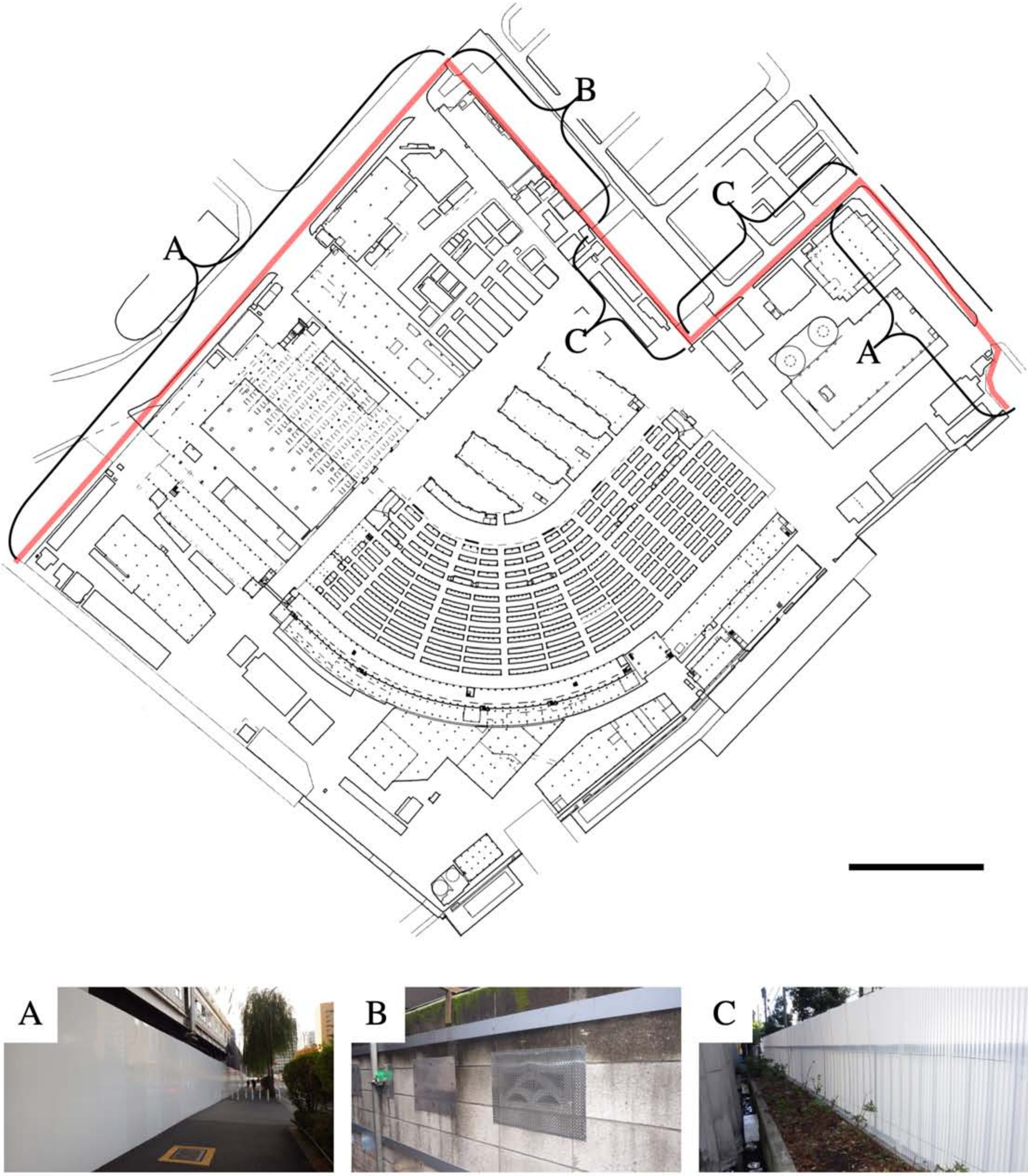


Fig. S6. Isolating wall details. The horizontal bar indicates 100 m.

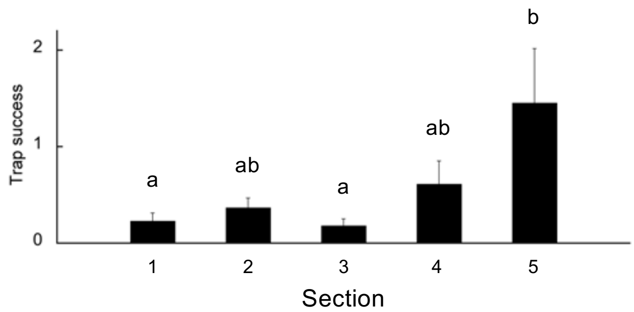


Fig. S7. Trap success in the five market sections from 12–17 October. The market was divided into 1) large- and mid-sized vegetable wholesalers, 2) processing plants and restaurants, 3) parking, seafood freezing warehouses, and associated trash collection areas, 4) large-sized seafood wholesalers, fish and shellfish tanks, and associated trash collection areas, and 5) mid-sized seafood wholesalers. Different letters indicate significant differences between groups ($P < 0.05$) as determined by one-way ANOVA followed by Tukey–Kramer HSD post hoc test (mean ± SEM).

Table S5. Spearman's rank correlation coefficient between factors.

	Year	Month	Day of culling	Trap success	Number of foreign tourists in Japan	Total trading volume	Total precipitation	Average daily temperature	Average daily high temperature	Average daily low temperature	Highest temperature	Lowest temperature	Average daily humidity	Lowest humidity	Sunlight hours
Year	1.00	-0.07	0.00	0.72	0.97	-0.92	-0.09	0.29	0.31	0.26	-0.14	0.29	0.36	0.26	0.51
Month	-0.07	1.00	0.00	0.25	0.14	-0.29	0.58	0.87	0.87	0.87	0.87	0.87	0.88	0.87	-0.43
Day of culling	0.00	0.00	1.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trap success	0.72	0.25	0.26	1.00	0.75	-0.80	0.30	0.46	0.49	0.43	0.13	0.49	0.52	0.44	0.18
Number of foreign tourists in Japan	0.97	0.14	0.00	0.75	1.00	-0.96	0.00	0.49	0.50	0.46	0.05	0.47	0.56	0.46	0.43
Total trading volume	-0.92	-0.29	0.00	-0.80	-0.96	1.00	-0.21	-0.61	-0.64	-0.57	-0.18	-0.59	-0.65	-0.54	-0.29
Total precipitation	-0.09	0.58	0.00	0.30	0.00	-0.21	1.00	0.45	0.46	0.43	0.45	0.45	0.40	0.50	-0.36
Average daily temperature	0.29	0.87	0.00	0.46	0.49	-0.61	0.45	1.00	0.99	0.99	0.78	0.88	0.95	0.90	-0.20
Average daily high temperature	0.31	0.87	0.00	0.49	0.50	-0.64	0.46	0.99	1.00	0.96	0.77	0.90	0.95	0.86	-0.21
Average daily low temperature	0.26	0.87	0.00	0.43	0.46	-0.57	0.43	0.99	0.96	1.00	0.77	0.85	0.95	0.93	-0.18
Highest temperature	-0.14	0.87	0.00	0.13	0.05	-0.18	0.45	0.78	0.77	0.77	1.00	0.61	0.70	0.79	-0.09
Lowest temperature	0.29	0.87	0.00	0.49	0.47	-0.59	0.45	0.88	0.90	0.85	0.61	1.00	0.95	0.77	-0.45
Average daily humidity	0.36	0.88	0.00	0.52	0.56	-0.65	0.40	0.95	0.95	0.95	0.70	0.95	1.00	0.91	-0.24
Lowest humidity	0.26	0.87	0.00	0.44	0.46	-0.54	0.50	0.90	0.86	0.93	0.79	0.77	0.91	1.00	-0.04
Sunlight hours	0.51	-0.43	0.00	0.18	0.43	-0.29	-0.36	-0.20	-0.21	-0.18	-0.09	-0.45	-0.24	-0.04	1.00

Colored cells indicates significant correlations between factors. Red and green indicate positive and negative corerlations, respectively.