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RESEARCH ARTICLE

Proximity to anthropogenic food sources determine roosting and nesting prevalence of feral pigeons (*Columba livia*) in a tropical city

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Abstract

1. The feral pigeon (*Columba livia*) is a globally commensal bird that can cause disamenities such as soiling and is a potential vector of various diseases. Aside to limiting food as a management strategy, reducing the availability of roosting and nesting sites can help regulate feral pigeon populations. Despite their prevalence, current knowledge of their roosting and nesting preferences is lacking.
2. Feral pigeons commonly use railway viaduct expansion gaps in Singapore for roosting and nesting. These gaps provided an ideal experimental platform to examine feral pigeon roost and nest site selection while controlling for differing cavity sizes which can significantly affect their reproductive success and site selection decisions. We also conducted an in-situ experiment to test the efficacy of nest removal as a management option.
3. Our nationwide surveys of 80.3 km of railway viaducts and 6048 gaps revealed that feral pigeon day roosting and nesting preferences are influenced by structural height and more importantly, their proximity to human food sources. There was a significantly higher probability of feral pigeon roosting in a gap if it had more pigeon feeding incidences in its vicinity and was higher. The probability of feral pigeon nesting in gap was higher if it was closer to a railway station, lower and further from water bodies.
4. In our field experiment, we did not find any significant differences in the proportions of the abundances of feral pigeon to other urban commensal bird species at the gaps before and after nests were removed.
5. Overall, our results suggest that a concerted effort to reduce anthropogenic food availability to feral pigeons is central in limiting their reproductive success and controlling their population.

KEYWORDS
bird, breeding, infrastructure, invasive, rock pigeon, site selection, urban commensal, wildlife management

1 | INTRODUCTION

Globally, invasive alien species, have brought about far-reaching negative effects on biodiversity (Bellard et al., 2016), ecosystem functioning and services (Vitousek et al., 1996), human health (Ogden et al., 2019), and the economy (Diagne et al., 2021; Pimentel et al., 2001). In Southeast Asia, the cost of environmental, economic, and health impacts caused by 151 invasive alien species has been estimated to be US$25.8–39.8 billion annually (Nghiem le et al., 2013). Of these species, the cost attributed to feral pigeon (*Columba livia*) alone was estimated to be US$83.8–209.3 million annually. The feral pigeon is probably one of the world's oldest and most widespread commensal bird species occurring through Southeast Asia (BirdLife International, 2021; Yap & Sodhi, 2004). They are descendants of wild rock pigeons that are native to Europe, North Africa and parts of Asia (Lowther & Johnston, 2020), and have adapted well to urban environments because man-made infrastructures are highly similar to their natural habitat (Ali et al., 2013; Ferman et al., 2010; Johnston & Janiga, 1995; Stukenholtz et al., 2019). Tall buildings with ledges are common roosting and loafing sites (i.e., a roost location where birds rest only in the day), while recesses in roofs and bridges are often used for nesting (Haag-Wackernagel & Geigenfeind, 2008; Johnston & Janiga, 1995). Feral pigeons have also been documented to forage on a wide variety of food, including handouts by feeders, food litter, accidental food spillage and grass seeds from lawns (Johnston & Janiga, 1995; Lim & Sodhi, 2004; Murton et al., 1972; Soh et al., 2021). As a consequence, pigeon populations in cities with an abundance of food, nesting and roosting sites have risen steeply (Giunchi et al., 2012; Stukenholtz et al., 2019; Tang et al., 2018).

Large pigeon populations in cities are known to bring about disamenities such as the soiling of buildings and urban infrastructure, which can in turn bring about serious chemical damage to their surfaces (Bassi & Chiatante, 1976; Spennemann et al., 2018). An individual pigeon can produce up to 12 kg of excrement annually (Rashotte et al., 1997; Spennemann & Watson, 2017). Pigeon excreta is known to habour at least 110 different human pathogenic organisms, of which seven are zoonotic such as *Chlamydophila psittaci* and *Cryptococcus neoformans*, which can bring about pneumonia, fungemia, peritonitis, encephalitis, histoplasmosis and various other diseases (Haag-Wackernagel & Moch, 2004; Magnino et al., 2009; Trofa et al., 2008). The excreta can also contain ectoparasites, such as mites and ticks, that can migrate to human hosts (Haag-Wackernagel, 2005). In Southeast Asia, feral pigeons are a widespread nuisance species in agricultural farms (Yap & Sodhi, 2004). Feral pigeons are also carriers of *Tricomonas gallinae*, a fatal avian disease, which may pose a threat to native pigeons and doves and raptors that prey on infected individuals (Alrefaei, 2020; Peh, 2010).

As a consequence of the potential negative impacts posed by feral pigeons, much effort has gone into the management of pigeon population in cities. The main strategies that have been applied to tackle pigeon overpopulation are direct population control and resource management through the reduction of food, roosting and nesting sites (Murton et al., 1972; Soh et al., 2021; Yap & Sodhi, 2004). Various studies have shown that key to the management of pigeon population is the limitation of anthropogenic food (Haag-Wackernagel, 1995; Jacob et al., 2014; Sol & Senar, 1992, 1995). Food reduction has been shown to hamper reproductive success and survival of both young and parents in bird species (Martin, 1987; Stock & Haag-Wackernagel, 2016). In Singapore, feral pigeons foraged for longer periods of time due to a reduction of anthropogenic food waste during the COVID-19 pandemic, which would likely hamper their reproductive success (Soh et al., 2021). Concomitant to limiting food as a management strategy, reducing the availability of nesting and roosting sites can also regulate pigeon population (Haag-Wackernagel & Geigenfeind, 2008; Reynolds et al., 2019). Feral pigeons were found to nest mainly in taller buildings in residential areas, possibly as a means of avoiding predation and disturbance (Fernández-Maldonado et al., 2017; Savard & Falls, 1981; Tang et al., 2018). Sacchi et al. (2002) also found that there was a positive relationship between feral pigeon abundance and flock number, and the number of old buildings in Milan, Italy. These buildings were constructed of bricks and hence had a greater availability of crevices for nesting and roosting.

In Singapore, feral pigeons are probably the most abundant urban commensal bird species. The probability of sighting a pigeon in Singapore increased from 55% in 2000–2001 to 62% in 2010–2011 based on a study using time-limited line transects (Chong et al., 2012). The current population for feral pigeons in Singapore is estimated to be 190,000 (95% CI ~130,000 to 250,000) pigeons (Tang et al., 2018). Feral pigeon feeding incidences, open-air food centres (typically located on the ground floor with easy public access from outside) and refuse collection centres contributed greatly to the anthropogenic food available to pigeons (Soh et al., 2021; Tang et al., 2018). In response, a campaign was launched by the government to raise awareness on the consequences of feeding wildlife (Ong, 2019). Government agencies are also working with municipal town councils to ensure proper food waste management at food establishments and enforce against littering. While much of the efforts have been focused on limiting their food resources, a successful management plan for any urban cospecies requires a multi-pronged approach that also addresses the availability of nesting and roosting sites.

We investigated the use of railway viaduct expansion gaps by feral pigeons for nesting and roosting in Singapore. These extensive above-ground viaducts are part of the Mass Rapid Transit (MRT) system, a principal mode of public transport for many Singaporeans. The MRT network began operations in November 1987 and is the most expansive metro system in Southeast Asia covering 261 km across the entire island, with a daily ridership of 3.4 million passengers in 2019. Other than the height of the viaducts, the numerous expansion gaps present in the MRT viaducts have similar dimensions. This provides an ideal experimental platform to examine the influence of viaduct structures and spatial distribution of their resources on the use of expansion gaps by pigeons on feral pigeon nest or roost selection, while controlling for confounding factors associated with differing cavity sizes.

Cavity sizes in trees or anthropogenic structures such as pipes and crevices in buildings vary considerably and can significantly affect decisions in selecting nesting or roosting sites and reproductive success (Di Sallo & Cockle, 2022; Lambrechts et al., 2013; Rendell & Robertson, 1989). Furthermore, most ecological research on feral pigeons have been conducted in temperate countries and temperature has been found to have considerable impacts on their reproductive biology (Hetmański & Wołk, 2005; Ryan, 2011). However, the urban ecology of feral pigeons in the tropics is less understood. Aside from a single study conducted in a desert city in Argentina, there are no other studies to our knowledge that has examined the nesting preferences of feral pigeons in urban environments (Fernández-Maldonado et al., 2017).

For our study, we first compared the occurrences of feral pigeons in the expansion gaps with other species. Next, we examined the influence of environmental (i.e., food resource and landscape effects) and structural factors on the nest and day roost (i.e., pigeons resting in the day) site selection of feral pigeons. Distance to food sources and predator avoidance have direct consequences on the fecundity and survival of offspring (Hetmański & Wołk, 2005; Martin, 1995). Hence, we hypothesise that the probability of pigeon using an expansion gap for nesting or roosting will be higher when (a) the gap is nearer to open-air food centres or anthropogenic food sources at the MRT stations, and closer to a higher frequency of pigeon feeding incidences; and (b) the gap is higher from the ground to avoid potential predators or threats from below since aerial predators of feral pigeons such as falcons are uncommon in the urban areas of Singapore (Lim, 2009). We also identified current and potential hotspots of feral pigeon and nest occurrence so that structural modifications can be made to deter the usage of these gaps. Finally, we conducted an in-situ experiment to test the efficacy of nest removal as a management option.

2 | MATERIALS AND METHODS

2.1 | Bird roosting and nesting survey

We conducted our surveys on bird roosting and nesting along all above-ground MRT tracks on the main island of Singapore (1°21′ N, 103°49′ E) from January to February 2020 and repeated our surveys in March 2020. Nest surveys were not conducted in the subsequent survey as the occurrence of new nests between February and March 2020 was expected to be minimal. Our surveys were conducted during the dry phases of the Northeast Monsoon with less rainfall and coinciding with the start of the breeding season for resident birds in Singapore (Lim, 2009). In total, 80.3 km of North–South and East–West viaducts amounting to 6048 gaps, were surveyed (Figure 1). For each viaduct gap, we measured the height of the gap from the ground (mean, 6.33 m), and recorded the state of deterrent measure used at the gap ('absent', 'present', or 'damaged'), as well as the presence or absence of nesting materials and soiling as an indication of bird usage (Figure 2). We also noted the bird species observed in the gap. Surveys were conducted in clear weather (i.e., non-rainy days) from 0900 to 1900 h. For gaps that were inaccessible because the viaduct cut across construction sites or private properties, we recorded the height of the gap only, and bird species occurring at the gap (~4% of the total number of gaps).

2.2 | Nest removal experiment

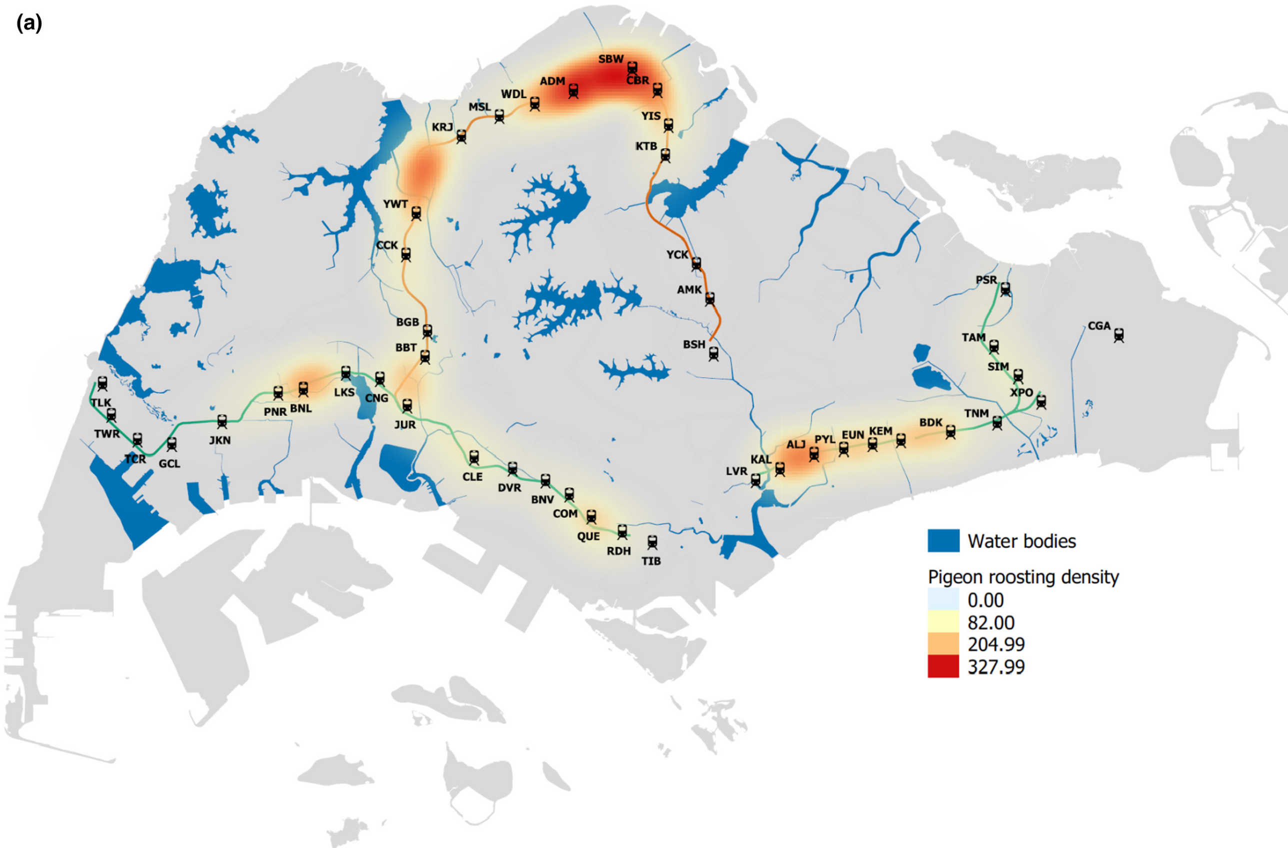
In our nest removal experiment, all nests found in 98 expansion gaps in the vicinity of Sembawang MRT station were removed by external contractors on 6, 8 November and 16 December 2020. Although these surveys did not coincide with the peak resident bird breeding period in Singapore, feral pigeons here were observed to breed throughout the year (Paperna & Smallridge, 2002). Furthermore, the schedule of our surveys was constrained by the availability of our contractors. We recorded feral pigeon abundances in gaps where nests were removed and not removed. The gaps where nests were not removed extended beyond both sides of the treatment gaps ($n = 184$). Urban commensal bird abundances were observed in three phases: before (26, 30 October 2020), approximately a month (27 January 2021), and 3 months after (27 April 2021) nest removal completion. Surveys were conducted on fair weather days from 0700–1000 and from 1600–1900 in all phases.

2.3 | Variables chosen for roost and nest-site selection

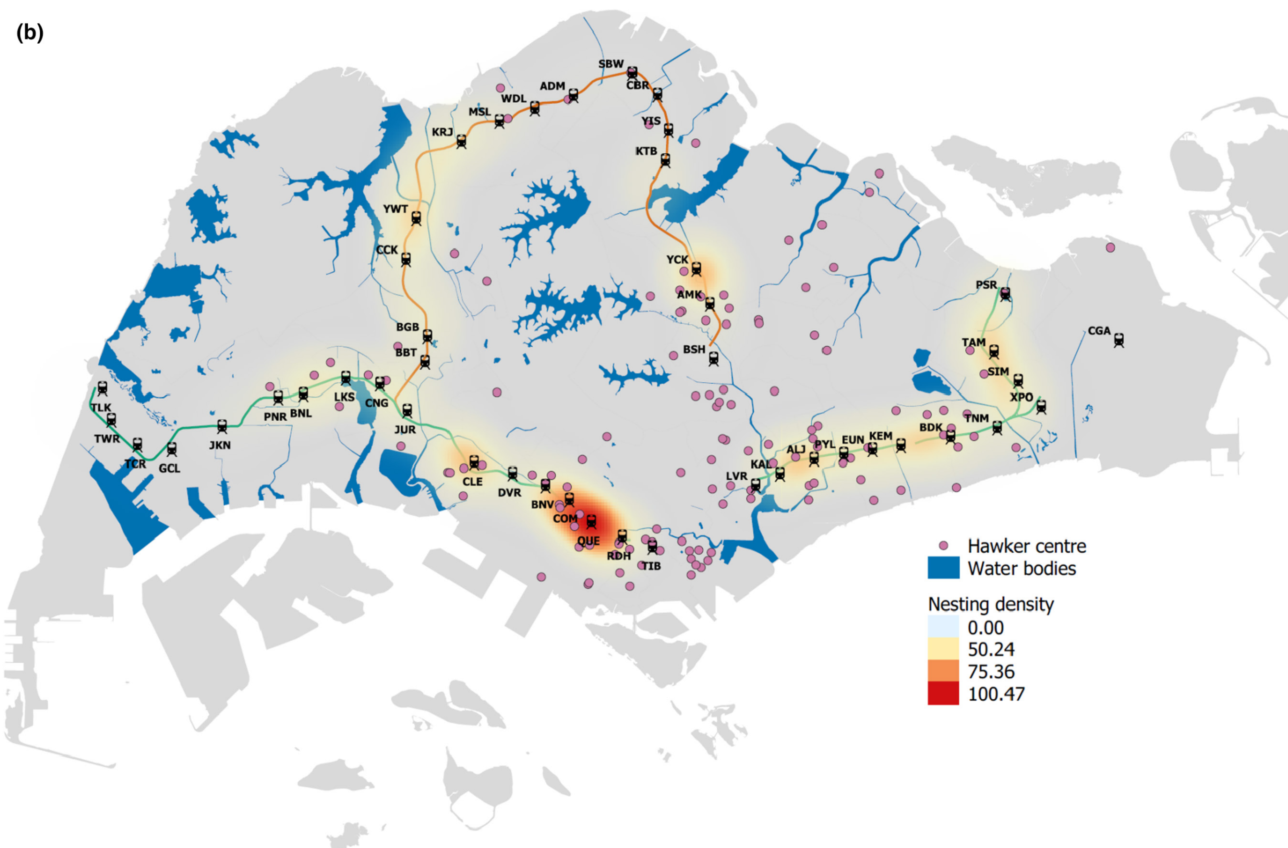
We observed a total of 2264 columns and 6048 viaduct gaps in 80.3 km of above-ground viaducts (Figures S2 and S3). For consistency, we only used 1751 columns that supported four expansion gaps for analyses. To minimise spatial autocorrelation, we selected 230 columns that were spaced at least 100 m apart from each other, beyond the feral pigeon natal distance of 90 m (i.e., maximum distance travelled by juvenile birds from their nests; Johnston & Janiga, 1995, Murton et al., 1972). Only columns that did not have any deterrent installed were selected because they may exclude pigeons from using the gaps. We aggregated the total number of feral pigeons detected in the four gaps of each column to obtain abundance since these gaps were connected. Feral pigeon day roosts were defined as gaps where the presence of a feral pigeon was recorded in least one of our two sampling occasions (i.e., January–February 2020 and March 2020), and showed an indication of nesting or soiling to preclude gaps that were only used only momentarily (e.g., as a hideout from a potential threat). The presence of nesting materials in the viaduct gaps such as twigs and leaves were used as an indication feral pigeon nesting. Any nests that included the presence of bird species other than the feral pigeon were omitted from analysis on feral pigeon nesting preferences.

We selected the following environmental and structural factors that may influence day roost and nest site selection of pigeons along the viaduct:

(a)


SBW
ADM
CBR
WDL
MSL
KRJ
YIS
KTB
YWT
CCK
YCK
AMK
BGB
BBT
BSH
PSR
CGA
TAM
SIM
XPO
TLK
LKS
CNG
PNR
BNL
JUR
TNM
BDK
KEM
EUN
PYL
ALJ
KAL
LVR
TWR
JKN
TCR
GCL
CLE
DVR
BNV
COM
QUE
RDH
TIB
Water bodies
Pigeon roosting density
0.00
82.00
204.99
327.99

(b)


SBW
ADM
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WDL
MSL
KRJ
YIS
KTB
YWT
CCK
YCK
AMK
BGB
BBT
BSH
PSR
CGA
TAM
SIM
XPO
TLK
LKS
CNG
PNR
BNL
JUR
TNM
BDK
KEM
EUN
PYL
ALJ
KAL
LVR
TWR
JKN
TCR
GCL
CLE
DVR
BNV
COM
QUE
RDH
TIB
Hawker centre
Water bodies
Nesting density
0.00
50.24
75.36
100.47

FIGURE 1 Distribution of feral pigeon roosting (a), and nesting (b) sites across North–South and East–West above-ground Mass Rapid Transit viaducts of Singapore, visualised using kernel density estimation. Density of roosts and nests are indicated by the colour intensity. Abbreviated and full station names are arranged on the East–West line in green followed by the North–South line in red: ADM, Admiralty; ALJ, Aljunied; AMK, Ang Mo Kio; BBT, Bukit Batok; BDK, Bedok; BGB, Bukit Gombak; BIS, Bishan; BNL, Boon Lay; BNV, Buona Vista; CBR, Canberra; CCK, Choa Chu Kang; CLE, Clementi; CNG, Chinese Garden; COM, Commonwealth; DVR, Dover; EUN, Eunos; GCL, Gul Circle; JKN, Joo Koon; JUR, Jurong East; KAL, Kallang; KEM, Kembangan; KRJ, Kranji; KTB, Khatib; LKS, Lakeside; MSL, Marsiling; PNR, Pioneer; PSR, Pasir Ris; PYL, Paya Lebar; QUE, Queenstown; RDH, Redhill; SBW, Sembawang; SIM, Simei; TAM, Tampines; TCR, Tuas Crescent; TIB, Tiong Bahru; TLK, Tuas Link; TNM, Tenah Merah; TWR, Tuas West Road; WDL, Woodlands; XPO, Expo; YCK, Yio Chu Kang; YIS, Yishun; YWT, Yew Tee.

FIGURE 2 (a) Feral pigeon using an expansion gap despite wire mesh installed at a Mass Rapid Transit viaduct. (b) Feral pigeon in an expansion gap with damaged bird spikes. (c) Javan mynas observed at an expansion gap. (d) Columns supporting viaducts with feral pigeons foraging on the grass nearby.

a. Intensity of pigeon feeding. "Mercy feeding" is a significant food source of pigeons in several cities (Murton et al., 1972; Ryan, 2011), including Singapore (Soh et al., 2021; Tang et al., 2018). Data for public feedback cases on mercy feeding (i.e., incidences where intentional feeding of pigeons by people occurred and were reported by feedback providers) were obtained from the National Parks Board (NParks) from January 2019 to January 2020 ($n = 3130$) and aggregated within a 300 m radius of each column.
b. Distance to nearest hawker centre. Hawker centres are food centres housed in open-air complexes made up of several small stalls selling cooked food. Urban commensal birds such as the house crow (*Corvus splendens*), Javan myna (*Acridotheres javanicus*) and feral pigeon have been found to be attracted to food wastes in the hawker centres (Lim et al., 2003; Soh et al., 2002, 2021). Here, we recorded the distance of each column to their nearest hawker centre.
c. Distance to nearest water body. Water is essential to feral pigeons, particularly during breeding for the production of crop milk (Johnston & Janiga, 1995). Feral pigeons were also observed to nest and roost near water points in cities (Ali et al., 2013; Rao & Koli, 2017). Water bodies in our study include rivers, reservoirs, and large canals.
d. Distance to nearest MRT station. MRT stations often have food outlets and their refuse collection points could also serve as a food source for feral pigeons. Thus, we calculated the distance from each column to the nearest MRT station.
e. Mean distance to nearest five public residential buildings. We chose five buildings to better represent a collective contribution at the estate level as opposed to an individual building. Tall buildings are favoured by feral pigeons for roosting or nesting on the ledges or roofs to avoid predation and disturbances (Ferman et al., 2010; Przybylska et al., 2012; Sacchi et al., 2002; Tang et al., 2018). Tall buildings were also highly correlated to pigeon density in Singapore (Tang et al., 2018). Here, we focused on public housing buildings, which are homes for most Singaporeans and typically range between 20 to 40 storeys high. We calculated the mean distance to the nearest five public housing buildings as our covariate.
f. Height of MRT viaduct expansion gap. A measure of the structural height of the available nesting or roosting sites. Feral pigeons tended to nest or roost higher to avoid predator and other disturbance from the ground (Fernández-Maldonado et al., 2017; Savard & Falls, 1981).
g. Observation time. We calculated the minutes passed from our earliest observation, which was at 0900 h, to the time each gap was observed.

2.4 | Statistical analyses

We used general linear model (GLM) with binomial error distribution and cauchit link function to determine the effect of environmental and structural covariates on pigeon day roosts and nesting in viaduct gaps. We also included the interaction between distance to nearest hawker centre and water body as a predictor since a similar interaction was shown to influence site selection in pigeons (Fernández-Maldonado et al., 2017). For our day roost GLM, we included observation time to account for within day variations in feral pigeon sightings. All covariates were standardised and retained in our models since none showed high collinearity (VIF <3) and standardised (scaled to the mean of 0 and standard deviation of 1; Kock & Lynn, 2012). The most parsimonious model was determined using Akaike Information Criterion corrected for small sample sizes (AIC_c; Burmham & Anderson, 2002). We chose cauchit link as it had the lowest AIC_c value among other link functions (i.e., log, logit, probit, cloglog) and its robustness to possible outliers (Koenker & Yoon, 2009). Moran's *I* correlograms for our day roost and nest GLMs indicated that columns in some distance bands were spatially autocorrelated (Figure S1). As such, we refitted our most parsimonious models using spatial (generalised linear mixed model) GLMMs since GLM functions cannot account for spatial autocorrelation. Spatial GLMMs also performed more favourably in accounting for spatial autocorrelation compared to other approaches (Dormann et al., 2007). We assigned our random effect to a single group and applied an exponential distance decay function to compute the spatial error. Spatial autocorrelation was reduced after refitting our models (Figure S1).

To validate our most parsimonious model, we examined binned residual plots which are suited for assessing models with binary outcomes (Kasza, 2015). Our model assumptions were validated our residuals resided within 95% confidence limits (Figure S2). Additionally, we conducted model averaging for candidate models with $\Delta AIC_c < 2$ after standardising all covariates (Thomas, 2017). Model averaging produces two models using different methods; the full average model indicates the weighted average of the parameter estimates for each model including parameter estimates of zero, while the conditional average model excludes them (Grueber et al., 2011). We drew our inferences from the conditional average model since we were interested in assessing the relative effects of all our covariates and thus avoided shrinkage towards zero for predictors with weaker effects in the full average model (Grueber et al., 2011).

We conducted Fisher's Exact tests to determine if there were significant differences in the proportions of feral pigeons to other urban commensal bird species detected at the expansion gaps before and after nest removal. Fisher's Exact were chosen over Chi Square tests since some of the expected cell counts were less than five. All analyses were conducted in RStudio, version 1.3.1056 (RStudio Team, 2020). We used the following R packages: *car* (v3.0-12) for calculating VIFs (Fox & Weisberg, 2019), *ncf* (v1.3-2) for computing Moran's *I* (Bjornstad, 2022), *MuMIn* (v1.46.0) for model selection and model averaging (Bartoń, 2022), MASS (v.7.3-58.2) for fitting spatial GLMMs (Venables & Ripley, 2002), and *arm* (v1.12-2) to examine the variance of standardised residuals (Gelman et al., 2021).

3 | RESULTS

Five bird species were observed using these viaducts, of which feral pigeons were by far the most abundant followed by Javan mynas (Figures 2 and 3). A total of 3921 pigeons were observed at the viaducts over the two surveys (first: 1981; second: 1940), occupying 22.8% of the gaps (Table 1). Highest average pigeon abundance was observed along Yew Tee-Kranji (190 pigeons) and Admiralty-Sembawang (158 pigeons) stations of the North–South Line (Figure S3). Despite the high abundance recorded, tracks near these stations did not show high pigeon densities likely due to the greater distances between stations along this line (from kernel density estimates in Figure 1).

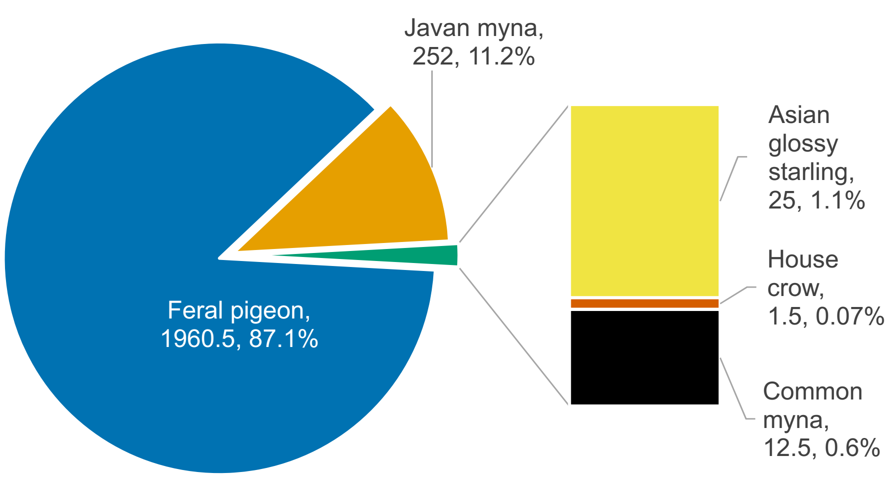

FIGURE 3 Average species abundance detected over two survey periods.

Our most parsimonious model showed that the probability of pigeon using a gap for roosting increased significantly, if it was higher and had a higher incidence of pigeon feeding within 300 m radius of the gap ($p<0.05$, Table 2; Figure 4). In our conditional average model, the probability of feral pigeon roosting in a gap increased significantly if it was higher and had a higher intensity of feral pigeon feeding which relates to a greater number of mercy feeding incidences ($p<0.05$, Table 2).

A total of 1021 nests were observed across the 6051 individual gaps. Nesting was observed to be relatively uniform along the North, South and East, and less prevalent in the West of Singapore (Figure 1). High nesting density was observed along Redhill to Commonwealth stations (Figure 1), while Yew Tee-Kranji had the highest number of nests with 92 nests observed (Figure S4).

Our most parsimonious model showed that the probability of pigeon nesting within an expansion gap increased if it was nearer a MRT station, lower and further away from a water body (Table 3; Figure 4). However, only distance to the nearest MRT station showed a significantly negative effect. Similarly, in our conditional average model, the probability of feral pigeon nesting in a gap increased significantly the closer it was to the MRT station ($p<0.05$, Table 3).

Feral pigeon abundance in gaps where the nests were removed showed a steady decline after nest removal (Figure 5). Conversely, their abundances in all gaps increased slightly, suggesting that the removal of nests in gaps merely caused the pigeons to occupy neighbouring gaps (Figure 5). We did not find any significant differences in the proportions of feral pigeon to other urban commensal bird species (i.e., Javan and common mynas) abundances observed at the gaps between the 3 months of surveys for gaps where nests were removed (Fisher Exact test, $p=0.53$, $n=98$) and gaps which also included nests that were not removed (Fisher Exact test, $p=0.93$, $n=282$; Figure 5).

TABLE 1 Frequency distribution of the abundance of pigeons observed in each gap over two survey periods. A total of 12,086 gaps were observed.

Number of pigeons in gap	Number of gaps	Percentage (%)
0	9325	77.16
1	1906	15.77
2	641	5.30
3	150	1.24
4	48	0.40
5	8	0.07
6	6	0.05
7	1	0.01
8	1	0.01

4 | DISCUSSION

Feral pigeons were observed using the expansion gaps much more than other species possibly due to their dominance over smaller commensal bird species such as the Javan and common mynas. Also, the expansion gaps may bear some resemblance to the sheltered cliff-edges which constitute the natural nesting habitat of the Mediterranean rock pigeons in the wild (Lowther & Johnston, 2020; Figure 2). Further, the Javan and common mynas have different nesting preferences and broader opportunities that extend beyond building structures such as tree cavities (Arazmi et al., 2022; Lowe et al., 2011).

Feral pigeons preferred day roosts that were associated with a higher frequency of feeding events in the vicinity, which suggested

TABLE 2 Parameter estimates of the most parsimonious spatial generalised linear mixed model and model-averaged general linear models with the probability of feral pigeon roosting in a viaduct gap as the response variable. All covariates were standardised. Superscripts * and ** indicate significant differences at $p<0.05$ and <0.01 respectively. There was a significantly higher probability of feral pigeon roosting in a gap if had more incidences of feeding.

Model type/covariates	Coefficient estimate	Standard error	*t*-Value/ *z*-value	*p*-Value
Most parsimonious model				
Intercept	0.57	0.16	3.51	0.0005**
Intensity of pigeon feeding	0.43	0.19	2.19	0.03*
Column height	0.15	0.16	0.98	0.33
Conditional average model				
Intercept	0.54	0.15	3.52	0.0004**
Intensity of pigeon feeding	0.52	0.26	2.00	0.046*
Column height	0.23	0.15	1.57	0.12
Distance to nearest Mass Rapid Transit station	−0.15	0.13	1.21	0.22
Observation time	−0.15	0.13	1.14	0.26
Distance to nearest water body	−0.15	0.14	1.08	0.28
Distance to nearest hawker centre	−0.11	0.13	0.83	0.41

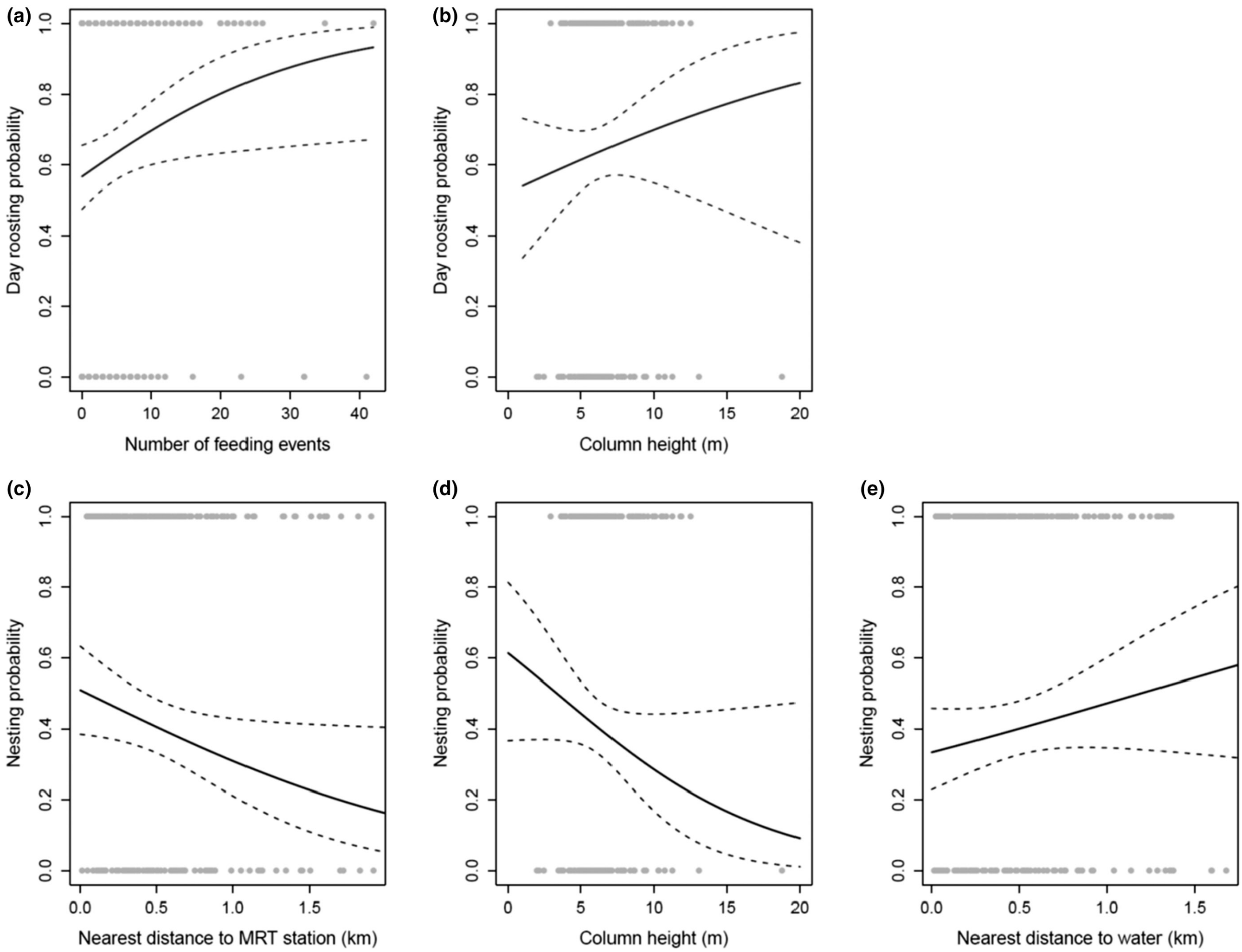

FIGURE 4 (a) Feral pigeon day roosting probabilities in viaduct gaps with respect to the number of feral pigeon feeding events within 300 m of the gap and (b) the height of the column supporting the expansion gap. (c) Feral pigeon nesting probabilities in gaps with respect to the distance to the nearest Mass Rapid Transit (MRT) station, (d) height of the column supporting the expansion gap, and (e) nearest water body. Predictions were made from the most parsimonious model. Grey dots represent the observed occurrences. Dotted lines represent 95% confidence intervals.

that proximity to food sources was desirable to optimise foraging efficiency (MacArthur & Pianka, 1966). Our findings are consistent with studies in Singapore and Basel, Switzerland, that showed mercy feeding to be a key determinant of feral pigeon local abundance (Haag-Wackernagel, 1993; Tang et al., 2018). The most parsimonious model for feral pigeon nesting preferences was also associated with food sources, but unlike the model for day roosts, they preferred nesting closer to a more predictable food supply. MRT stations which have food stalls where feral pigeons have been observed to regularly congregate, often near common refuse collection points feeding on food scraps on the ground. Additionally, high human traffic in train stations also increases the likelihood of food litter in the vicinity. Likewise, in Basel, breeding female pigeons with GPS receivers were found to travel beyond the vicinity of the city to forage on more abundant and predictable food in agricultural areas, in view of the higher energy demands for reproduction (Rose et al., 2006). Feeders, on the other hand, represent an uncertain food source since pigeon feeding is an offence in Singapore and enforcement can deter further feeding. Persons found feeding feral pigeons are liable to be fined up to SGD 10,000. Given the closeness and abundance of anthropogenic food, and the safe and conducive environment that the viaduct gaps provide (Batisteli et al., 2021), the survival rate and reproductive capacity of feral pigeons using such gaps for nesting may be close to optimal (Li & Martin, 1991; Martin & Roper, 1988; Murton et al., 1972; Shakov & Kövér, 2020). Although, feral pigeons can nest on open surfaces, such as on building ledges and roof tops, adaptable bird species in urban environments may prefer to nest in cavities that ensure a higher reproductive success due to lower predation pressure and possibly controlled temperatures (Hetmański & Wołk, 2005; Karpińska et al., 2022).

The structural heights of gaps also influenced roosting and nesting decisions, but to a lesser degree relative to food proximity. Feral pigeons preferred roosting in gaps that were higher, consistent with an earlier study in Poland where feral pigeons occurred in

TABLE 3 Parameter estimates of the most parsimonious spatial generalised linear mixed model and model-averaged general linear models with probability of feral pigeon nesting in viaduct gap as the response variable. All covariates were standardised. Superscripts * and ** indicate significant differences at $p < 0.05$ and <0.01 respectively. There was a significantly higher probability of feral pigeon nesting in gap nearer to a Mass Rapid Transit (MRT) station.

Model type/covariates	Coefficient estimate	Standard error	*t*-Value/*z*-value	*p*-Value
Most parsimonious model				
Intercept	−0.41	0.16	−2.51	0.01*
Distance to nearest MRT station	−0.35	0.18	−2.03	0.04*
Column height	−0.28	0.16	−1.71	0.09
Distance to nearest water body	0.22	0.16	1.36	0.18
Conditional average model				
Intercept	−0.42	0.14	2.92	0.004**
Distance to nearest MRT station	−0.38	0.19	2.06	0.04*
Column height	−0.27	0.17	1.57	0.12
Distance to nearest water body	0.21	0.14	1.42	0.15
Distance to nearest hawker centre	−0.25	0.22	1.14	0.26
Intensity of pigeon feeding	0.10	0.13	0.76	0.45
Distance to nearest hawker centre × water body	−0.20	0.25	0.78	0.44
Distance to nearest 5 public residential blocks	0.07	0.25	0.26	0.79

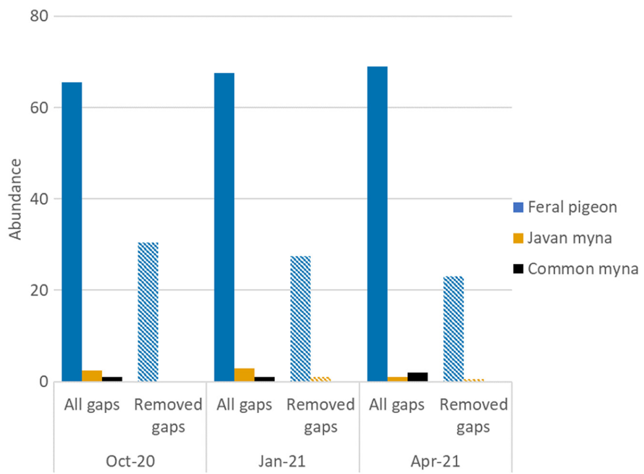

FIGURE 5 Solid coloured bars represent the total commensal bird abundance averaged over two surveys in 282 viaduct gaps where nests were removed and *not* removed during the nest removal experiment. The nests were removed from 6 November to 16 December 2020. Bars with diagonal lines represent the total urban commensal bird abundance averaged over two surveys in 98 viaduct gaps where nests were removed during the nest removal experiment. No significant differences in the proportions of feral pigeon to other commensal bird species abundances were observed at these gaps between the 3 months.

higher densities on taller buildings (Przybylska et al., 2012). Higher perches likely allowed the pigeons to keep a distance away from potential threats below, including people and predators (e.g., feral cats or rats; Jarvis, 2010). Moreover, higher vantage points may enable individuals to scan their surroundings further for foraging opportunities (Greig-Smith, 1983). Conversely, there was a higher probability of feral pigeons nesting in expansion gaps that were lower. This observation could be an indirect consequence of intraspecific competition with feral pigeons using gaps for roosting. Unoccupied gaps near an abundant food source may be in short supply, constraining breeding pigeons to nest in gaps that are comparatively lower and yet sufficiently high to provide a sense of security. Such a hypothesis could be tested with manipulative field experiments involving the removal of roosting feral pigeons in gaps close to an abundance of food and observing if breeding pigeons will subsequently use such gaps.

Our model indicated that feral pigeons preferred nest sites further from water bodies unlike a similar study in San Juan, Argentina (Fernández-Maldonado et al., 2017). The water bodies in our study consist of reservoirs and rivers that represent less developed areas with forests in water catchments. Hence, feral pigeons will probably nest closer to more developed areas away from these large water bodies given their preference to anthropogenic food (Soh et al., 2021). That said, feral pigeons do need a nearby water source for drinking and bathing, and will more likely use smaller open drains. In the San Juan study, the water bodies consisted of water fountains which are shallow and thus enabled the pigeons to drink and bathe while our reservoirs, rivers and large canals are too deep (Fernández-Maldonado et al., 2017).

Feral pigeon nesting distribution did not necessarily mirror their day roost distribution. Localities with higher nesting densities were not necessarily indicative of higher day roost densities (Figure 1).

This could be due to nesting and roosting pigeons selecting gaps based on different human food source types. Abundant and predictable food supplies at the MRT stations are more desirable than handouts that are less certain and transient (Rose et al., 2006), and as such, gaps closer to more reliable food sources are more likely to be occupied by breeding pairs (Bosè et al., 2012). The spatial disparities in nest and roosting sites may therefore reflect a strategy to reduce intraspecific competition between breeding and non-breeding adults or juveniles (Clay et al., 2016).

In both day roost and nest site selection of feral pigeons, proximity to food was a key factor and the long-term approach to slowing population growth should be centred on reducing their anthropogenic food supply (Fernández-Maldonado et al., 2017; Haag-Wackernagel, 1993; Soh et al., 2021; Yap & Sodhi, 2004). This includes continued enforcement against pigeon feeding, and limiting food waste in food outlets. Since September 2021, the return of trays, crockery and food litter at hawker centres and other food outlets has been enforced and repeat offenders are liable to be fined up to SGD 2000 (Raguraman & Tay, 2021). While the move will inevitably improve cleanliness and reduce the abundance of urban commensal birds in food and beverage establishments, such measures can curb the reproductive success of feral pigeons and other species of urban bird commensals due to a lack of sustenance (Sumasgutner et al., 2014). Additionally, reducing the feeding of feral pigeons should go beyond enforcement. A clearer understanding of the motivations behind pigeon feeding can help agencies to better educate the public against feeding them (Clark et al., 2019; Cox & Gaston, 2016). While studies conducted in other countries have suggested several plausible reasons such as deriving a psychological benefit, showing care, or manifesting an inclination towards nature, cultural differences may underlie alternative motivations behind pigeon feeding in Singapore (Cox & Gaston, 2016; Reynolds et al., 2017). Thus, surveys conducted in Singapore would provide a local and more informed perspective on the motivations behind pigeon feeding.

As shown in our in-situ experiment, nest removal will have no long-term bearing on their attempts to breed, as they are likely to occupy the viaduct gaps nearby. Thus, nest removal is likely an ineffective measure in limiting their reproductive capacity. Further, females have been found to respond to egg removal by increasing their reproduction attempts (Jacquin et al., 2010). Feral pigeons can also nest in similar expansion gaps in road bridges, attics of old shophouses and air conditioner ledges in high rise buildings (Sacchi et al., 2002). Hence, deterrence measures, for example, wire meshes will only serve to exclude their occurrences locally with limited impact on population growth as nesting opportunities are abundant. Nonetheless, installing such physical deterrents can be considered at viaduct gaps closer to the railway stations with higher human traffic to reduce dis-amenities such as soiling which may pose a health risk (Haag-Wackernagel & Geigenfeind, 2008). This could also be prioritised for gaps that are higher (e.g., height > 11 m from the ground for 0.75 occupancy, Figure 4). That said, regular maintenance of any bird repellent structures is needed to ensure their continued effectiveness since several observed during our surveys were damaged, suffered from corrosion or had fallen off.

5 | CONCLUSIONS

Singapore's railway viaducts represented a unique opportunity to determine if feral pigeons were selecting for optimal nesting and roosting sites by limiting the distances travelled to their foraging sites, while minimising confounding effects of differing nesting conditions such as size and microclimate. Our nationwide surveys revealed that feral pigeon day roosts and nesting preferences are influenced by structural height and more importantly, their proximity to human food sources. Thus, a concerted effort to reduce anthropogenic food availability to feral pigeons is central in limiting their reproductive success and controlling their population.

AUTHOR CONTRIBUTIONS

Kai Ning Lim: Data curation, formal analysis, project administration, investigation and writing—original draft; Malcolm C. K. Soh: Conceptualization, formal analysis, methodology, validation, supervision and writing—original draft; Duncan Y. W. Leong: Data curation, writing—review and editing; Adrian H. B. Loo and Benjamin P.-H. Lee: Writing—review & editing; and Kenneth B. H. Er: Supervision, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Moran's *I* correlograms of model residuals using 500 m distance lags for feral pigeon (A) day roost and (B) nest presence binomial general linear models. Unfilled circles represent non-significant spatial autocorrelation ($p \geq 0.05$). (C) and (D) show the same but using residuals from binomial generalised linear mixed models that account for spatial autocorrelation.

Figure S2. Binned residual plots for feral pigeon (A) day roost and (B) nest binomial generalised linear mixed models adjusted for spatial autocorrelation. Abbreviations are defined in Figure 1.

Figure S3. Average pigeon abundance with standard error bars between stations along all above-ground North–South and East–West lines, arranged from highest to lowest. Abbreviations are defined in Figure 1.

Figure S4. Number of gaps with nesting materials observed between Mass Rapid Transit stations along the North–South Line and East–West Line, arranged from highest to lowest.

Table S1. General linear models for predicting presence of feral pigeon day roosting and nesting respectively in a viaduct gap as the response variable and their associated Akaike information criterion values.

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