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Factors limiting the current distribution of the introduced Java sparrow (*Lonchura oryzivora*) in Bangkok, Thailand

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Abstract. Alien species invasions are often characterised by stages: transport, introduction, establishment, and finally invasive spread, but not all established alien species succeed in expanding, and reasons for their differing relative success are not well documented. Although widely introduced, the Java sparrow (*Lonchura oryzivora*) is endangered in its native range (Java and Bali). Free-ranging Java sparrows were first reported in northern Bangkok, Thailand, 90+ years ago. They have an established breeding population, but have not spread beyond this area. We investigated the present distribution, habitat use, and nest survival of the Java sparrow population in Bangkok to obtain a greater understanding regarding its lack of expansion. Forty-one 400 ha grid cells were randomly selected from northern Bangkok, a primarily urban area interspersed with paddyfields. Field surveys were conducted February 2017–July 2017 and nest observations during August 2016–August 2017. Java sparrows were detected in 37.5% of grid cells, but the detection rate was low (2.8% of surveys). Models suggested that Java sparrows preferred areas with smaller paddyfields closer to roosting sites rather than larger patches of paddyfields further from nesting or roosting sites. All nest cavities were in buildings or other artificial structures; roosts were in trees. Nest survival was 49%. However >50% (41 of 78) of nesting attempts were abandoned; they were also displaced from five of 67 nest sites by native species. Lack of expansion was possibly caused by low reproductive rates, perhaps exacerbated by nest-site competition from native species. Given the low probability of invasive spread and relative similarity of bird communities in Bangkok and in the Java sparrow's native range, this Bangkok population may have potential conservation value as reintroduction stock for the species.

Key words. introduced species, habitat use, *Lonchura oryzivora*, species management

INTRODUCTION

Non-native species often have negative impacts on the native ecosystems to which they are introduced including crop damage, displacement of native species, hybridisation with native congeners, disease transmission, disturbance to urban/human settlements as well as other impacts (Martin-Albarracin et al., 2015; Menchetti et al., 2016; Thibault et al., 2018). The process of alien species invasions is often divided into four stages: transport, introduction, establishment, and finally invasive spread. But not all established alien species succeed in expanding, and some remain restricted to specific areas (Murgui, 2001). There are likely multiple factors in these novel environments, both biotic and abiotic, that could determine the geographical spread (or lack thereof) of non-native species (Blackburn & Duncan, 2001; Lockwood et al., 2013). These include presence of suitable habitat, climate matching and native competitors/predators (Elton, 2000; Bomford et al., 2009, 2010; Strubbe & Matthysen, 2009). Alteration of any of these factors would likely affect the spread of introduced species and thus studies of these factors would assist our understanding of the invasion process (Vall-llosera et al., 2016).

The Java sparrow (*Lonchura oryzivora*; Family Estrildidae) is native to Java and Bali and has been introduced to multiple regions of the world (i.e., Thailand, Peninsular Malaysia, Hawaii, Venezuela, Columbia, Fiji, and other countries) (Clement et al., 1993; Del Hoyo et al., 2010) through releases during religious ceremonies (Agoramoorthy & Hsu, 2007) and the pet trade (Round, 1990; Brooks-Moizer et al., 2009; Donegan, 2013). This finch feeds on grain and nests in natural and/or man-made cavities (Restall, 1997). Most regions that Java sparrows were introduced such as Singapore and Hong Kong, colonies have established themselves (Gibson-Hill, 1950; Carey et al., 2001; Sodhi & Sharp, 2006) but have not spread. Further, the population in Singapore appears to have been extirpated due to unknown causes (Lim, 2009). In Thailand, Java sparrow has been reported in the wild in Bangkok since 1924 (Riley, 1938) with no data available on the size of founder population. There have been relatively few reports regarding the size of the trade in Java sparrow, although McClure & Chaiyaphun (1971) reported 10,256 Java sparrows, which included 2,984

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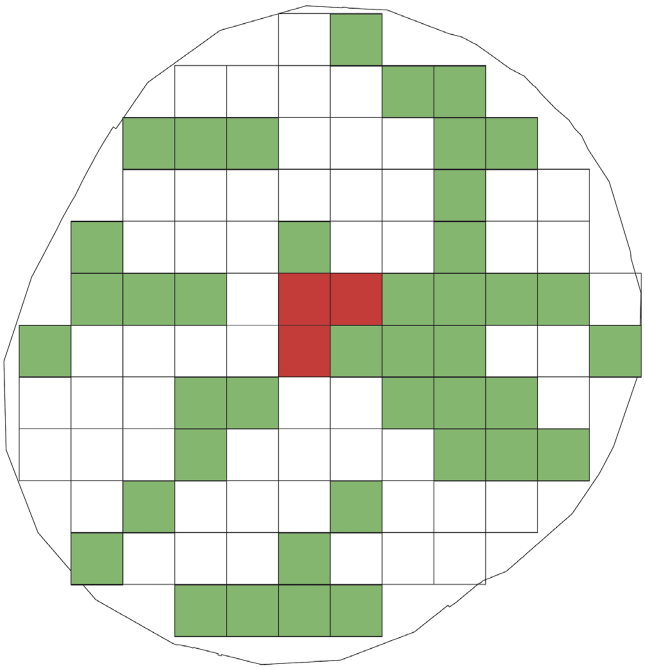

Fig. 1. 101 grid cells (400 ha each) were overlaid on the study area (40,000 ha). We randomly selected approximately 40% (41) (green) of 98 accessible grid cells in total. Access to three grid cells (red) in the middle of study area including Don Muang International Airport were restricted by the Thai Air Force.

albino morphs at a pet market in Bangkok. In 1987–1988 Round (1990) in a repeat survey of the same market found only 587 sparrows. Round & Gardner (2008) reported that the sparrow's range in Thailand was still mainly confined to the vicinity of the Don Muang Airport (located in northern Bangkok; 13.9133° N, 100.6042° E) and nearby districts. However, the Bangkok distribution of Java sparrow has not been investigated in detail and the reasons for the lack of expansion of this exotic species away from northern Bangkok over the past 90 years, despite the likely availability of suitable habitat, are unknown. Java sparrow is Red Data Book-listed (Globally Endangered) in its native range that means introduced populations of Java sparrows are also of potential conservation importance (Gibson & Yong, 2017; BirdLife International, 2018).

This study aimed to collect data on two baseline population parameters, namely population size and reproductive success, and then further investigate the possible limitations on the expansion of the Java sparrow in northern Bangkok by assessing its current distribution and habitat use. We hypothesised that the distribution of Java sparrow was limited by available foraging patches within residential areas of Bangkok.

MATERIAL & METHODS

Study site. The study was conducted in northern Bangkok, including the districts of Bang Khen (13°52′N, 100°35′E), Don Muang (13°54′N, 100°35′E), Lak Si (13°53′N, 100°34′E), Sai Mai (13°55′N, 100°38′E), Khlong Sam Wa (13°51′N, 100°42′E); and nearby provinces, Nonthaburi, Muang District (13°51′N, 100°30′E) and Pak Kret District (13°51′N, 100°42′E); and Pathum Thani, Muang District (14°1′N, 100°32′E) and Lam Luk Ka District (13°55′N, 100°44′E). The total area covered by the study was approximately 40,000 ha. The western side of the study area lies close to the Chao Phraya River and was almost entirely urban. The north-western and southern parts of the study area were also dominated by urban areas, while some sections to the east were still dominated by paddyfields. The average annual rainfall was approximately 1,511 mm per annum during 1987–2017 (Don Muang Airport Meteorology Station). Access to some areas adjacent to the airport in Don Muang district was restricted by the Royal Thai Air Force.

Bird surveys. Using a geographic information system (GIS) (QGIS Development Team, 2018), a total of 101,400 ha grid cells were overlaid on the study area (Fig. 1) (access to three grid cells in the middle of study area was forbidden by the Royal Thai Air Force). A total of 41 grid cells were randomly selected. For each selected cell, five straight transects (400 m length each) were randomly set and surveyed five times for 35 minutes on each occasion from February 2017–July 2017. There was one surveyor per transect. All study transects were covered on foot along roads, which were primarily on flat terrain. Each survey was conducted randomly during one of three daytime periods: 0700–1000 hours, 1100–1400 hours or 1500–1800 hours. Java sparrow was searched by visual surveys. When a Java sparrow was detected, the observer counted the total number of individuals within a flock and recorded the following parameters: date and time of detection, habitat (human-made structures such as buildings, utility wires, pavement or vegetation such as trees, lawns, grasslands, paddyfields), behavior including, foraging, courtship or resting for up to 10 minutes or until they flew out of sight. The locations of all individuals or flocks were recorded by using a global positioning system (GPS).

Roost counts. Two major roosting sites of Java sparrow, previously well known to local bird watchers, (Kan Kheha Thung Song Hong and Chaeng Watthana, Lak Si district, Bangkok approximately 2 km apart; Fig. 2) were also counted to estimate population size. Direct counts at each site were conducted during 1800–1900 hours once per month (Yuda, 2008).

Spatial variables. Rice is one of the main food resources for estrildid finches (Del Hoyo et al., 2010). The cover of paddyfields was therefore a potentially important variable in predicting the distribution of Java sparrow and was obtained from GIS shape files obtained from the Thai Land Development Department (2015–2016). The distance from the two main roosting sites to the center of each grid cell was also assessed in our analysis. In addition, spatial dynamic variables that indicated fragmentation and isolation of paddyfields were calculated, including edge density, patch density and mean nearest neighbour distance of paddyfields in grid cells (Table 1). All variables were calculated using QGIS (QGIS Development Team, 2018) and the LecoS plugin (Jung, 2016) for spatial dynamic variables.

Table 1. Description of landscape variables measured from 41,400-ha grid cells for predicting the abundance of Java sparrow in and around Bangkok, Thailand. All variables were estimated by using QGIS software and the LeCos plugin for the spatial dynamic variables.

Variables	**Data type**	**Description**
Site variables		
Paddyfield area (Paddy)	Continuous	Total paddyfield cover (ha) in a given grid cell
Distance from roosting site (Roost)	Continuous	Distance from roosting site to center of each grid cell (km)
Spatial dynamic variables (landscape scale)		
Patch density (Patch)	Continuous	Number of paddyfield patches divided by the total area (ha)
Edge density (Edge)	Continuous	Total length (m) of paddyfield edge divided by total area (ha)
Nearest neighbour distance (Neighbour)	Continuous	The average distance between paddyfield patches within study grid cells (km)

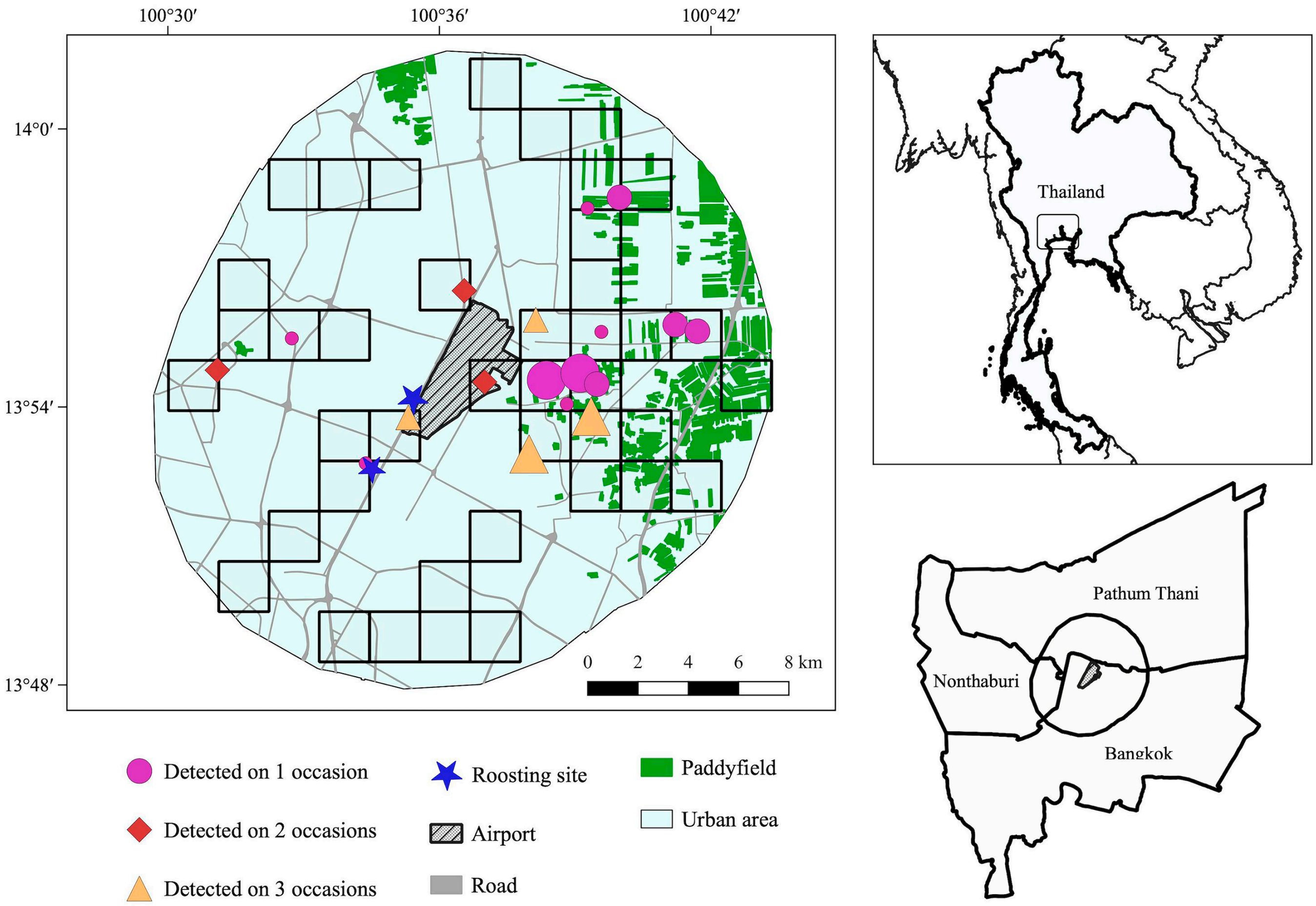

Fig. 2. Forty-one grid cells randomly set within a 10-km radius around Don Muang airport, Bangkok, Thailand, used for surveying Java sparrows. Don Muang was the site where Java sparrows were first recorded in Thailand in 1924. The study area includes three provinces; Bangkok, Pathum Thani, and Nonthaburi. The primary land use was urban, while paddyfields were mostly located on the eastern side of the study area. Different symbols (circles, squares and triangles) represent the number of occasions (out of 5 possible visits to a location) on which the sparrow was detected. Size of symbols of Java sparrow detection points was related to the number of birds detected; smallest size indicated only 1 bird was detected, medium size indicated 2–10 birds were detected, and largest size indicated a group of more than 40 birds was detected.

Statistical analysis. The effect of the spatial variables on the presence/absence of Java sparrow was tested using generalised linear mixed models (GLMMs) (Bolker et al., 2009). Grid cell ID number and survey replicate were classified as random effects. A pairwise-correlation matrix was used to test for multicollinearity among numeric variables (Zuur et al., 2010). Variable pairs with $r \geq \pm 0.5$ were tested separately in the models because of possible collinearity between pairs. There was a strong correlation between paddyfield cover and two variables, edge density ($r = 0.969$) and mean nearest neighbour distance ($r = 0.686$). Therefore, these variables were excluded from candidate models that contained paddyfield cover as a predictor to avoid biasing regression coefficient estimates (Zuur et al., 2010; Cade, 2015). Numeric variables were standardised to have 0 mean and unit variance (1 standard variation) before creating the set of candidate models (Gelman & Hill, 2014). The likelihood of candidate models was evaluated using differences in Akaike's Information Criteria (delta AIC) and Akaike weights (Burnham & Anderson, 2002). The 95% confidence intervals were used to recognise variables with substantial effects on Java sparrow presence/absence. The GLMM analysis was conducted in R version 3.4.1 (R Core Team, 2017) using lme4 package (Bates et al., 2015). AICcmodavg (Mazerolle, 2017) was used to assess model-averaged beta coefficients based only on the group of top-ranked models (delta AIC $\leq$ 6). Comparisons between the marginal R^2, R^2 of fixed effects and the conditional R^2 were used for assessing how well candidate models fitted the data (Nakagawa et al., 2017).

Nest observation. Nest site observations were conducted within a 4-km radius around Don Muang Airport, the primary area for historical records of Java sparrow as noted above. Observations were conducted during August 2016–August 2017. In addition, nest-sites reported by other birdwatchers were also checked. A nesting attempt was defined as when a bird was observed accessing a chamber or crevice with nest material such as dry or fresh grass, pieces of plastic, nylon, etc. Because Java sparrow in the study area nested mostly in private residential buildings, the outcome of each nesting attempt could only be determined from outside these buildings and using a camera on a pole when nests were reachable. In most cases, nest contents were not visible, but entrances could be clearly seen. Nesting activity of each nest site was observed for one hour every 3–4 days outside the days of the distribution surveys. Nest-accessing frequency by adults was observed: nesting activity was considered affirmed if birds accessed a nest cavity or accessed a nest cavity and remained inside (≥5 minutes). A nest was defined as 'active' if parent(s) were still showing nesting activity during a subsequent observation day (observed entering/leaving a cavity); 'failed' if no activity was recorded for 2 weeks after two or more previously observed active days; or 'abandoned' if, after a bird's initial access to a cavity with nest material, there was no subsequent activity. Nest stages were determined by observing the activities of the likely breeding adults (Martin & Geupel, 1993). Successful nests were defined as those active nest cavities with recently fledged young observed within 1 m of the entrance (Li & Martin, 1991). Daily mortality and nest success of all nesting attempts were evaluated using the Mayfield method (Mayfield, 1975; Hensler & Nichols, 1981) useful for obtaining unbiased estimates of nest survival when nests are likely to be found at various stages of the nesting cycle or possibly fail before they are discovered (Mayfield, 1975).

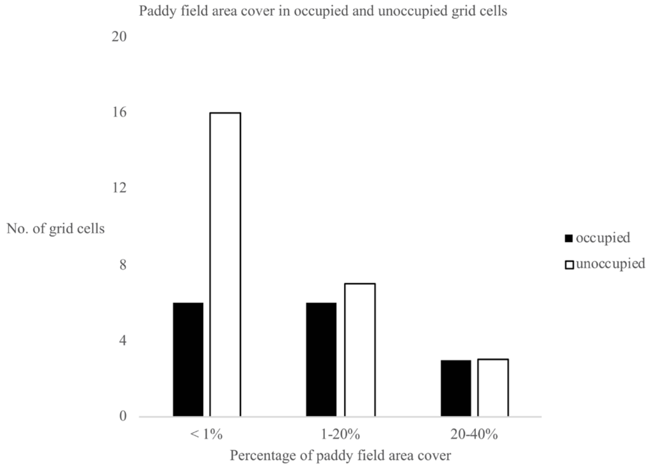

Fig. 3. Within the 15 occupied cells, 6 cells had a percentage of paddyfield cover < 1%, 6 cells had 1–20% paddyfield cover and 3 cells had 20–40% paddyfield cover. For the 26 cells with no detections, 16 had a percentage of paddyfield cover < 1%, 7 cells had 1–20% paddyfield cover and 3 cells had 20–40% paddyfield cover.

RESULTS

Habitat occupancy of Java sparrow. Surveys were conducted from February 2017 until July 2017 with 1025 replicates in 41 grid cells along 205 transects. Java sparrows were detected 29 times (2.8% of the replicates) in 15 of the 41 grid cells (37.5%) (Fig. 2). Percentage of paddyfield area cover are shown in Fig. 3. Distribution of paddyfield cover was not significantly different between occupied cells and cells with no detections (chi square = 2.3, $p = 0.49$, df = 3). Cells at the center of the study area had the highest number of Java sparrows. The 15 grid cells occupied by Java sparrow had a slightly larger mean area of paddyfield cover (36.3 ha ± SE 13.0) and were located closer to the two main roosting sites (7.45 km ± SE 0.9) than unoccupied cells (32.37 ha ± SE 11.6 and 9.33 km ± 0.6, respectively), but the differences were not statistically significant (paddyfield cover; t test = 0.2, $p = 0.8$ and roosting site distance; t test = –1.6, $p = 0.1$). Levels of fragmentation and isolation were not significantly different in occupied cells compared to cells without detections (Table 2). For 21 of the 26 unoccupied cells the land cover was entirely urban, whereas 13 of the 15 occupied cells were entirely urban, also not significantly different (chi square = 1.9, $p = 0.37$, df = 2). Java sparrows were mostly found in small groups (2–5 individuals) (15 times) or as single individuals (10 times) (~86% of detections), and on 4 occasions they were found in groups of more than 40 individuals (14% of detections). On three of these four occasions they were observed foraging in paddyfields where the highest count was 70 individuals.

Table 2. Summary statistics of land cover types and spatial dynamic variables between grid cells with Java sparrow detections (n =15) and grid cells without detections (n = 26).

Land cover and spatial dynamic variables	**Detected cells**				**Undetected cells**				**T test**	
	Mean	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	**t**	**P**
Paddyfield area cover (ha)	36.29	13.01	0	147.41	32.37	11.69	0	233.80	0.22	0.82
Distance from roosting site (km)	7.45	0.96	0.14	14.11	9.33	0.6	1.94	14.50	–1.65	0.11
Patch density (no. of patches/total area)	3.25	1.39	0	18.74	1.16	0.46	0	9.84	1.42	0.17
Edge density (m/ha)	12.9	4.05	0	45.63	10.62	3.49	0	60.02	0.42	0.67
Nearest neighbor distance (km)	0.32	0.10	0	0.96	0.25	0.07	0	1.06	0.54	0.59

Table 3. Model selection of Java sparrow abundance (with delta AIC ≤ 6) in relation to landscape and spatial dynamic variables in the study area. 'K' represents the number of estimated parameters. Variables used in these models included paddyfield cover (Paddy), distance from roosting site (Roost), paddyfield patch density (Patch), paddyfield edge density (Edge), mean nearest neighbour distance of paddyfield in grid cells (Neighbour). Variables in parenthesis indicate random effects.

Model (33 models tested)	**K**	**AIC**	**ΔAIC**	**AIC weight**	**Marginal R^2**	**Conditional R^2**
Roost + Neighbour | (grid)	5	306.01	0.00	0.27	0.218	0.681
Roost + Patch | (grid)	5	307.28	1.27	0.14	0.166	0.696
Roost + Edge | (grid)	5	308.01	2.00	0.10	0.190	0.711
Patch | (grid)	4	309.38	3.37	0.05	0.085	0.713
Roost + Paddy | (grid)	5	309.49	3.48	0.05	0.147	0.728
Roost | (grid)	4	309.94	3.93	0.04	0.073	0.744
Null model	3	310.84	4.83	0.02	0	0.756
Neighbour | (grid)	4	311.16	5.14	0.02	0.050	0.721
Paddy + Patch | (grid)	5	311.45	5.44	0.02	0.086	0.712

Effect of spatial variables on Java sparrow abundance. None of the candidate models were strongly supported. However, distance to roost site (negative regression coefficient, i.e., a negative association), nearest neighbour distance (positive association), paddyfield patch density (positive), and paddyfield edge density (positive) had similar levels of modest support (Table 3). Using 95% confidence intervals, four of the five coefficients for four of five variables tested did not overlap zero, while one variable, paddyfield area was not significant, with intervals overlapping zero (Table 4).

Roost counts. Both lowest and highest counts during successive visits (33 and 2,132) were obtained from the Kan Kheha Thong Song Hong roost. The average number of birds at each roost was 1,023 (SE = 183.9) individuals at Kan Kheha Thong Song Hong and 487 (SE = 58.5) individuals at Chaeng Watthana. Number of birds at Kan Kheha Thong Song Hong had greater variance due to notably low number at initial counts. During the first month of the counts, branches of the roosting tree were trimmed, greatly reducing the number of birds using this roost, but numbers subsequently increased over the study period. Counts at Chaeng Watthana were smaller, although the numbers roosting were more stable after the first two months of counts (Fig. 4).

Nest survival. The breeding period of Java sparrow in Bangkok began in August and ended in March, with October having the most nesting attempts (20). A total of 78 nesting attempts at 67 nest sites were observed at four nest localities (Fig. 5). Bhumibol Hospital had highest number of nest sites while the lowest number was at the Thai Air Force Youth Club and Phahonyothin Soi 69/1 (Fig. 6). Birds usually built nests in crevices or chambers in buildings, ceiling holes, gaps between air ducts or chambers of exhibited airplanes in the Air Force Museum with several kinds of nest materials (e.g., fresh/dry grass, nylon, string, plastic). Twenty-seven active nest sites and 40 abandoned sites in four nesting areas were found between 2 August 2016 and 3 August 2017. At only 6 nests were we able to observe nest contents directly; three of which had eggs and the other three were observed during the nestling stage. In 41 of 78 nesting attempts at 40 nest sites, birds were seen accessing chambers/crevices with nest material, but no nest activity was detected on subsequent observations. In 37 nesting attempts at 27 nest sites, nesting activity was observed on multiple occasions.

Table 4. Estimates of coefficients of tested variables, standard errors (SE) and their 95% confidence intervals (CI) predicting presence/absence of Java sparrow in grid cells of the study site. Variables used in these models included paddyfield cover (Paddy), distance from roosting site (Roost), paddyfield patch density (Patch), paddyfield edge density (Edge), mean nearest neighbour distance of paddyfield in grid cells (Neighbour). Coefficients with confidence intervals not overlapping zero were considered statistically significant.

Variables	Coefficient	SE	Lower 95% CI	Upper 95% CI
Roost	–1.43	0.66	–2.73	–0.13
Neighbour	1.47	0.57	0.34	2.60
Patch	1.12	0.52	0.08	2.16
Edge	1.39	0.68	0.05	2.73
Paddy	1.15	0.72	-0.26	2.58

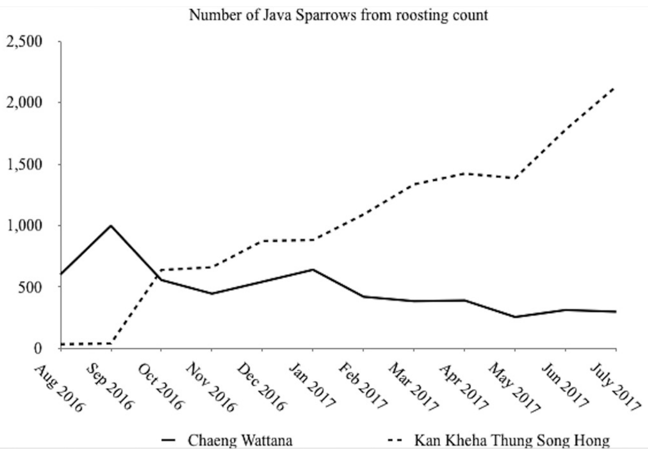

Fig. 4. Number of Java sparrows counted at the two main roosting sites in Bangkok, Thailand, each site was counted once per month from August 2016 to July 2017. Lowest and highest counts (33 and 2132 individuals) were obtained from the Kan Kheha Thung Song Hong (KKTSH) roost (dashed line). Lowest counts at KKTSH were in August–September 2016. The roosting site at Chaeng Wattana (solid line) had a lower number of birds but may have received some birds from KKTSH during the first two months of the count.

Second nesting attempts were observed at 8 nest sites and third nesting attempts from 2 nest sites. Twelve nesting attempts were successful, 13 attempts failed and 12 nests had unknown outcomes. Daily nest survival rate was 0.98 (SE = 0.004) and expected survival of the average nest was 0.49 (SE = 0.09).

Aggressive direct nest competition between Java sparrow and two resident species, great myna (*Acridotheres grandis*) and Eurasian tree sparrow (*Passer montanus*), was observed 12 times during surveys, resulting in the Java sparrows at two cavities each being displaced by Eurasian tree sparrow and by the myna during 17 October–26 December 2016. During 20 November 2016–3 February 2017, great myna occupied 3 further nest sites at the Bhumibol Hospital that had been previously occupied by Java sparrow.

Adult and juvenile mortality. During the survey, 10 dead birds were found: eight (three adults and five juveniles) died from apparent window strikes and two (one adult and one juvenile) were entangled by dangling building materials.

Feeding observations. Java sparrow was observed feeding on ripened rice at four locations out of the 29 times the finch was detected. In addition, they were also observed to feed on *Eriochloa procera* (Family: Poaceae) five times, *Dactyloctenium aegyptium* (Family: Poaceae) twice, *Acalypha indica* (Family: Euphorbiaceae) once and *Gomphrena celosioides* (Family: Amaranthaceae) once.

DISCUSSION

Habitat occupancy. Java sparrows were mostly found on the eastern side of the core area of the study site within 4 km of their initial point of detection approximately 90 years ago. Further, the detection rate was extremely low (29 detections from 1,025 transect surveys), suggesting that the Java sparrow has not spread and maintains a relatively small population considering the number of generations since its initial release.

From our analysis, candidate GLMMs with two-variable models had more support than single variable models (Table 3), while no single-variable model had clear support over our null model regarding Java sparrow habitat use (Table 3). However, all the top-ranked models had small marginal R^2 values and notably smaller than the conditional R^2 suggesting weak to no effects of the tested fixed effects (Table 3). A combination of spatial variables (edge density, patch density and mean nearest neighbour distance) and distance from roosting sites were associated with the occurrence of Java sparrows in the study area. In particular, Java sparrow foraged closer to the two main roost sites rather than points further away. A likely preference for feeding close to secure roosting or nesting areas may place constraints on the use of more distant paddies and other feeding areas (Gordon, 2000). Nearest neighbour distance and patch density showed positive effects suggesting that Java sparrows were more likely to be detected in grid cells where the paddyfields were more isolated and/or fragmented. Java sparrow is well-known as a consumer of grains, especially rice (Clement et al., 1993; Del Hoyo et al., 2010) and therefore we expected to find them in areas with clumped resources such as paddyfields. However, our data show that they do frequently forage on other kinds of seeds in abandoned grassy areas. Reports

Fig. 5. Four nest localities of Java sparrow in the study area; nurse dormitory of Bhumipol Hospital (1), Air Force Youth Club (2), Air Force Museum (3) and Phaholyothin 69/1 alley (4). Java sparrows were mostly found nesting in (1) and (3). All sites were located < 1.5 km from Don Muang Airport. (1), (2) and (3) were located on the eastern side of Don Muang Airport and (4) was located to the south-west.

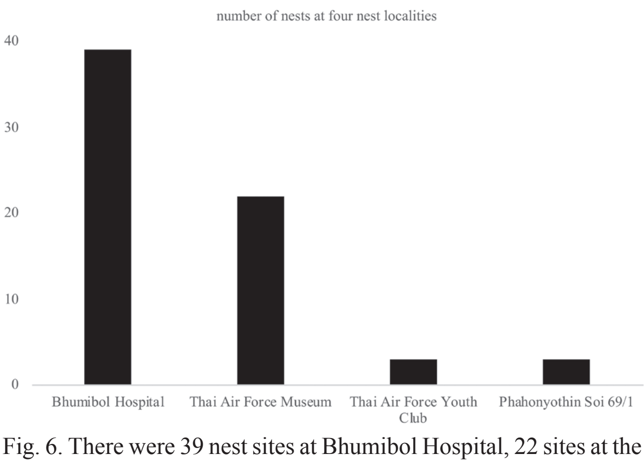

Fig. 6. There were 39 nest sites at Bhumibol Hospital, 22 sites at the Royal Thai Air Force Museum, 3 at the Thai Air Force Youth Club and 3 at Phahonyothin Soi 69/1. Birds mostly located their nests in cavities in the ceilings of buildings or in openings of air ducts.

of the natural foods of Java sparrows in their native and non-native range were scarce. Reports from experiments with captives show that a variety of seeds are taken by Java sparrows such as safflower (*Cartamus tinctorius*), Japanese millet (*Echinochloa frumentacea*), white millet (*Panicum miliaceum*), red manna seed (*Panicum maximum*) and canary seed (*Phalaris canariensis*) (van der Meji & Bout, 2000; Nagy Koves Hrabar & Perrin, 2002).

Currently, it is not clear from our data why Java sparrows would prefer more fragmented habitats, but it may suggest a preference for more heterogenous landscapes for foraging (Loyn, 1987) and may partly explain their unexpected low detection rate in larger paddyfields. Generally, size of a resource patch would positively affect occupancy and/or abundance, in contrast with fragmented and/or isolated resources (Debinski & Holt, 2000; Koleček et al., 2015). Agricultural habitats usually provide food resources before harvest, meanwhile after harvest, grasslands and/or other semi-natural habitat within agricultural landscapes could provide additional resources (Vickery et al., 2009). Furthermore, field boundaries are particularly heterogenous and habitat heterogeneity would be higher in landscapes with small fragmented agricultural areas compared to areas with larger paddyfields (Fahrig et al., 2015). Based on field observations, Java sparrows were typically found foraging on a variety of grass seeds, and it is likely that these resources are patchy in time and space (Wilby & Shachak, 2000) and thus heterogeneous landscapes may only contain a subset of habitat patches with suitable food sources at any given time. Moreover, heterogeneous landscapes that include buildings may be particularly suitable for this species as such landscapes may contain a combination of potential nesting areas together with foraging areas (Steele, 1993; Forschler & Kalko, 2006). However, ecologically similar Australian finches; black-throated finch (*Poephila cincta*) and Gouldian finch (*Erythura gouldiae*) appear to select nesting areas and foraging areas separately (Dostine et al., 2001; Rechetelo, 2015).

The main effects from the spatial variables we assessed appeared to be relatively weak as measured by R^2, suggesting that other habitat features may be important, or that the temporal and spatial scales of seed availability may have been finer than we could measure.

The detection rate of Java sparrows was extremely low and individuals were rarely found in successive visits to the same transect; this is also consistent with a species that feeds on temporary, unpredictable food resources along with perhaps rapid changes in the landscape, such as from construction, redevelopment and cutting of grasses (Newton, 1998). Theoretical studies suggest that temporal variation has more effect on population dynamics than spatial variation (Fahrig, 1992; Keymer et al., 2000; Matlack & Leu, 2007; Hodgson et al., 2009). The time-limited/temporal availability of preferred resources usually affects the abundance and dynamics of populations (Blake & Loiselle, 1991; Clergeau et al., 1998; McKinney et al., 2011; Rousseau et al., 2015). For example, Wells (1966) found that the fluctuation in abundance of three other estrildid finch species; white-headed munia (*Lonchura maja*), scaly-breasted munia (*L. punctulata*) and black-faced munia (*L. malacca*) was related to the availability of ripened rice before and after harvest.

Finally, more precise accounting for landscape structure and composition, such as natural/semi-natural grassland cover, riparian zone grass vegetation and other grassy vegetation in agricultural landscapes, together with GPS telemetry, may help to better understand foraging and distribution patterns of Java sparrows. This would also require the collection of fine-scale habitat data, perhaps assisted by high-resolution remote sensing, as currently, detailed GIS data are not available.

Nest survival. Nesting began in early August and ended in March. All nests were located in man-made structures (buildings, and cavities in airplanes on display at the museum). Expected nest survival of Java sparrow in this study was 49%. Our results of nest success appear to be relatively moderate but comparable with other estrildid finch species. For example, nest success of Gouldian finch (*Erythura gouldiae*) in natural woodland in Australia was 32–56% (Tidemann et al., 1999). In this study, we had only three nests in which we were able to observe nest contents directly, starting at the egg stage, and only one which was observed until the fledging stage. This was not enough to investigate clutch size, but this number was not higher than previous reports (2–12 eggs; Kurniandaru, 2008). Because of issues of access, we typically could not observe nest contents and did not video record nests, and thus we were unable to assess cause of failures. There were likely many causes of nest failure in our urban study area, including nest abandonment (Antonov & Atanasova, 2003; Blair, 2004; Barton & Holmes, 2007), nest predation from rats (Major et al., 1996; Matthews et al., 1999; Smith et al., 2016), insufficient protein sources for chicks (Seel, 1970; Peach et al., 2008) and interspecific nest site competition (Frei et al., 2015). Human disturbance in the form of noise pollution was also possibly responsible for nest abandonment in heavily urbanised areas (Ortega, 2012).

Nest site competition between Java sparrow and two native hole-nesters, great myna and Eurasian tree sparrow was observed and at least seven nest sites (~10% of those observed) were displaced by these native species. Native competitors are a kind of biotic resistance that could obstruct resource occupation by introduced species thereby reducing their geographic spread (Hart & Gardner, 1997; Elton, 2000; Levine et al., 2004; McKinney & Kark, 2017). For example, at least some nest sites of the exotic ring-necked parakeet (*Psittacula krameri*) in the Upper Rhine Valley, Germany were observed being taken over by native European starlings (*Sturnus vulgaris*) (Czajka et al., 2011). However, Eurasian tree sparrow and the endemic Javan myna (*Acridotheres javanicus*) both compete with Java sparrow in their native range in Java (Kurniandaru, 2008; Yuda, 2008; Arlott, 2018). Therefore, the observed competition in Bangkok was not surprising.

We conclude that the population of Java sparrows in Bangkok has grown slowly over the past 90 years starting presumably from a large, but unquantified founder population; a relatively large population is much more likely to avoid extinction (Soulé, 1987; Blackburn et al., 2015). Given its occurrence in Thailand for such a long period, our limited data suggest that its potential to become either an agricultural pest or a significant ecological competitor with native species is minimal. Its population is estimated at no more than approximately 2,500 individuals based on our roost counts. It is still largely confined to the same area as its initial release, and its reproductive rate seems relatively low. Moreover, it is subject to fairly intense interspecific nest-site competition from at least two very common native species. Nest site competition has been recognised as an important factor that can suppress reproductive rates (Dhondt & Frank, 1999; Frei et al., 2015), thus limit the spread of the species (Caswell et al., 2003). Based on our data, we suggest that its relatively slow reproductive rate may also be limiting the distribution of Java sparrow in Bangkok. Finally, given the Java sparrow's endangered conservation status in its native range and the general similarities of the bird communities between Bangkok and parts of its native range, our study population may now have long-term conservation value. For example, introduced Java sparrow populations may reduce pressures on native populations from the pet trade (Gibson & Yong, 2017). Therefore, the population should be monitored regularly (yearly) at the two main roost sites at least to assess population status and growth rates.

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