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Undesirable aliens: factors determining the distribution of three invasive bird species in Singapore

Haw Chuan Lim*, Navjot S. Sodhi*[1], Barry W. Brook† and Malcolm C. K. Soh*

*Department of Biological Sciences, National University of Singapore, Blk S2, 14, Science Drive 4, Singapore 117543, Republic of Singapore
†Key Centre for Tropical Wildlife Management, Northern Territory University, Darwin, NT, 0909, Australia
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Abstract. Biological invasions are a major environmental concern due to their negative impacts on biodiversity and economics. We determined the population sizes and habitat-abundance relationships of the three most successful invasive bird species in Singapore: the house crow *Corvus splendens*, white-vented myna *Acridotheres javanicus* and common myna *A. tristis*. Estimated population sizes of the three species between February 2000 and February 2001 were between 106 000–176 000, 122 000–155 000 and 20 000–29 000, respectively. Population size of the house crow grew dramatically (>30-fold) in the last 15–16 y while that of the white-vented and common myna declined. Habitat–abundance relationships suggest that house crows are highly dependent on anthropogenic food. Their abundance was also positively related to proximity to coast. The common myna associated closely with agricultural areas while the white-vented myna probably preferred urban greenery among residential buildings. Our study shows that the three invasive bird species associated with different aspects of human-modified environment.

Key Words: abundance, *Acridotheres javanicus*, *Acridotheres tristis*, *Corvus splendens*, habitat association, invasive species, urbanization

INTRODUCTION

The negative impact of biological invasions on native biodiversity is probably as far-reaching as global climate change and extensive clearance of natural habitats (Vitousek *et al.* 1996). Although not exclusively caused by humans, modern trade and transport have unquestionably facilitated the increase in biological invasions to an unprecedented level. Scientists and managers are not just interested in colonization of new areas by biological invaders, but also in their spread and persistence, as they often cause substantial environmental and economic damage as their densities increase (Mack *et al.* 2000, Sakai *et al.* 2001, Williamson 1996). Primentel *et al.* (2000) estimated that the current annual damage caused by biological invaders in the United States alone was around US$137 billion. Moreover, this damage included only economic losses and control costs, but did not take into account their damaging environmental effects.

Birds are a conspicuous component of the natural environment and have long been introduced by humans to different parts of the world for various reasons (e.g. hunting, nostalgia, biological control of pests; Long 1981). Sometimes introductions were inadvertent, such as through escapes from domesticity, as stowaways in ships (e.g. house sparrow *Passer domesticus*), or through range expansion mediated by extensive habitat modifications. There are many possible negative effects of introducing birds, including transmission of diseases/parasites to native birds, damage of human property (including cultivated crops), and competition or hybridization with native species (Bomford & Sinclair 2002, Lever 1987, Mooney & Cleland 2001).

We studied the distribution of three invasive bird species in the island state of Singapore. As a busy port, Singapore has a history of receiving non-native bird species since the 19th century. Gibson-Hill (1952) noted that there were around 13 non-native bird species in Singapore at that time. Six of the species occurred in low numbers ('isolated occurrences'), while the other seven species were more abundant and were known or presumed to be breeding (e.g. Java sparrow, *Padda oryzivora*). Lim & Gardner (1997) documented 20 established non-native bird species in Singapore, comprising about 10% of the number of resident bird species. We focused on the three most successful and potentially damaging invasive bird species: the house crow (*Corvus splendens* Vieillot), white-vented myna (*Acridotheres javanicus* Cabanis) and common myna (*A. tristis* Linnaeus).

The house crow's native range spans southern Iran to Thailand (Madge & Burn 1994). It is not only common

[1] Corresponding author. Email: dbsns@nus.edu.sg

in its native range but has invaded many towns and cities around the Indian Ocean in the last century (e.g. Aden, Djibouti and Mauritius; Long 1981). Ali & Ripley (1972) describe it as omnivorous, and concluded that its overall status in agricultural areas was neutral as it consumed both injurious insects and agricultural produce. In eastern Africa, house crows were known to pillage passerine nests (e.g. ploceids) and heronries. The crows also mobbed and harassed adult birds, and this probably resulted in the displacement of many native birds from their natural habitats (Archer 2001, Ryall 1992). In addition to the ecological damage, the house crow also inflicted economic damage by predating chicks and eggs (making free-ranging poultry impossible) and eating crops such as maize (*Zea mays*) and sorghum (*Sorghum vulgare*) (Archer 2001). Preliminary studies also showed that the faeces of house crows harbour pathogens (e.g. *Salmonella*) that can cause enteric disorders in humans (Jennings 1992).

In Singapore, the house crow frequently congregates in communal roosts near housing estates and urban areas. These roosts can contain upwards of 4000 crows and may persist for many years (Sodhi *et al*. 2001). The noise from such roosts, and the accumulated droppings, are a nuisance to residents who live nearby. When the crows gather to roost, they often perch on structures and buildings nearby, soiling them and sometimes damaging associated fixtures. During the breeding season, adult nesting crows occasionally attack passers-by (Soh *et al*. 2002). Although Lim & Gardner (1997) speculated that the house crow may be out-competing and causing the decline of the native large-billed crow (*C. macrorhynchos*), it is equally likely that the latter's decline is caused by a reduction in habitat (e.g. secondary forests, mangroves).

The white-vented myna is an endemic of Java, Bali and southern Sulawesi while the common myna originated from central and southern Asia (Feare & Craig 1998). The former appeared to have arrived in Singapore as escaped pet birds while the latter probably arrived through range expansion from the north as forests in Peninsular Malaysia were cleared (Gibson-Hill 1950, Ward 1968). In many places, the primary damage caused by these two mynas is the predation of cultivated fruits and young crops (Long 1981). The common myna is also known to compete for nesting cavities with hole-nesting bird species (Dhanda & Dhindsa 1996, Pell & Tidemann 1997*a*). The exotic mynas are hypothesized to be one of the factors leading to the decline of native hole-nesting oriental magpie robin (*Copsychus saularis*) in Singapore (Huong & Sodhi 1997). Since agriculture is not extensively practised in Singapore, the problem of the mynas as agricultural pests is not a major concern here. The main problems posed by the mynas, like the house crow, are the noise and droppings associated with communal roosts in urban areas, and competition with native bird species (Yap *et al*. 2002).

Due to the perception of the house crow and mynas as nuisance and pests, and potential threats to native fauna, a number of management-related studies have been carried out in Singapore (Brook *et al*. 2002, Hails 1985*a*, *b*; Peh & Sodhi 2002, Soh *et al*. 2002, Yap *et al*. 2002). However, the environmental variables conducive to the high abundance of these three invasive species have not been determined quantitatively. Here we identified and compared the environmental variables (e.g. food abundance, vegetation structures) affecting the abundance of the house crow, white-vented and common mynas in Singapore. Using historical data, we also determined how the populations of these three species have changed over time. We believe that such data will provide a more comprehensive ecological understanding of these three successful Asian invasive species.

METHODS

Study area

We conducted research in the Republic of Singapore (1°20′N, 103°50′E) which consists of one main island (591.4 km^2) and more than 50 smaller offshore islands. At the closest point, the main island is about 600 m away from Peninsular Malaysia. The climate is characterized by high temperature and relative humidity (mean daily: 26.8 °C and 84.3%, respectively), and high rainfall (approximate annual rainfall: 2344 mm) (Meteorological Service Singapore, http://www.gov.sg./metsin/). With the exceptions of granite hills in the centre of the island, very little land in Singapore has elevation above 61 m.

The main primeval vegetation type of Singapore was lowland evergreen rain forest, which originally occupied about 82% of the land area, with mangrove and freshwater swamp forests constituting the remainder (Corlett 1991). Since its modern founding in 1819, Singapore has become increasingly urbanized, and now has one of the world's densest populations, at 5900 persons km^{-2} (Singapore Department of Statistics, http://www.singstat.gov.sg/). As the need for land to provide for human habitation intensified, primary and tall secondary forests dwindled to about 1700 ha while built-up areas now account for about 50% of the land area (Corlett 1992). Maintained alongside these built-up areas are an assortment of green spaces, urban parks and golf courses which cover an estimated total area of around 106 km^2 (Corlett 1992). Farmland in Singapore has been reduced from a high of about 300 km^2 in the 1940s, to about 130 km^2 in the 1960s (Corlett 1992). It was further reduced to only about 75 km^2 in 1981 and 9.8 km^2 in 2000 (Singapore Department of Statistics, http://www.singstat.gov.sg/).

Bird counts and historical data

To estimate bird abundance, we surveyed 30 fixed-width line-transects, each 500 m long and 100 m wide. Each

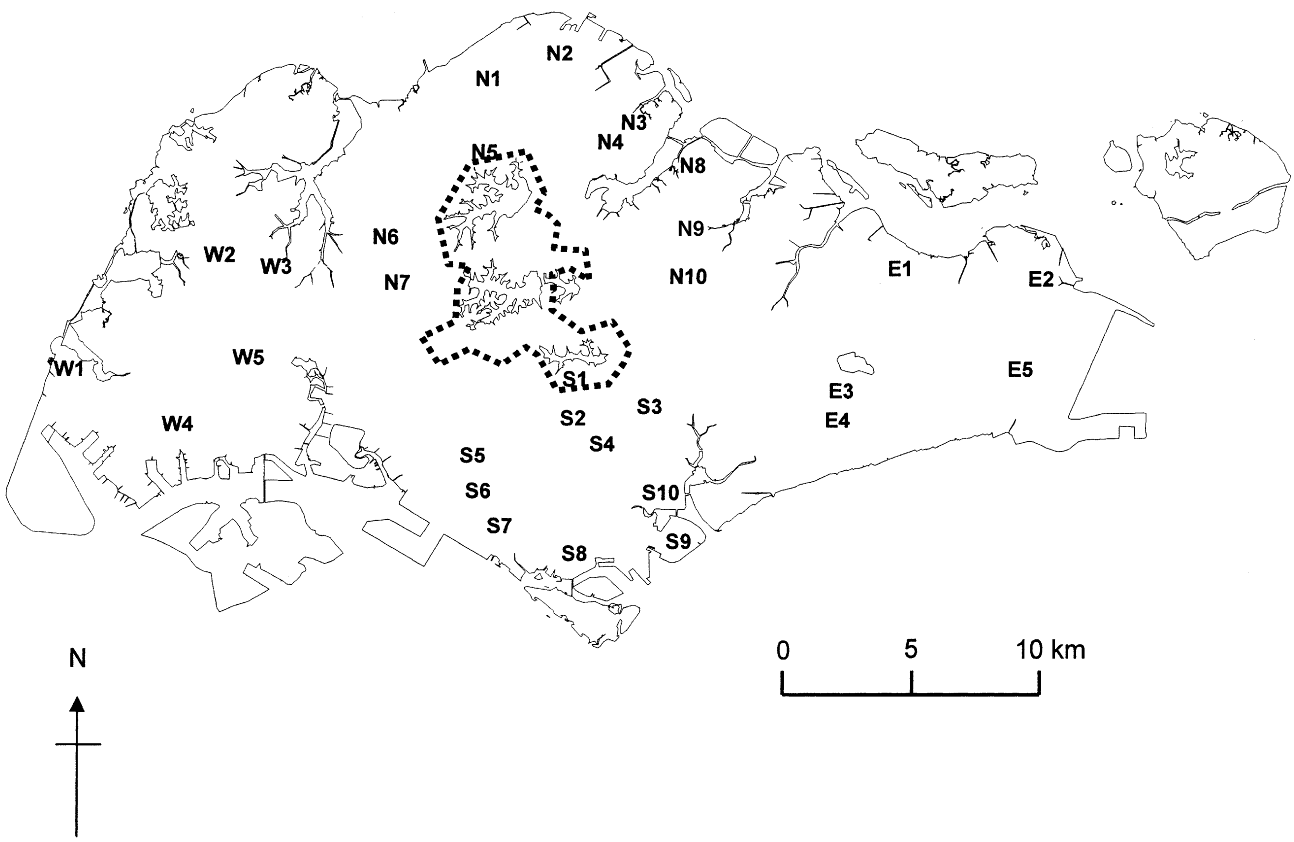

Figure 1. Map of Singapore showing bird survey transects (e.g. N1) on the main island. Letters before numbers indicate the survey section the transects fell in: N = north, S = south, E = east and W = west. Hatched lines show approximate extents of central nature reserve that is covered by primary or tall secondary rain forests.

transect was surveyed six times and all transects were located on the main island of Singapore. We stratified the sampling by dividing the island into four regions: north, south, east and west (Figure 1). There were ten transects in each of the first two regions while the latter two regions contained five transects each. The amount of accessible area in the eastern and western regions was smaller because of the presence of airports and military areas. Locations of the sampling sites were randomly selected using street directory grids but the exact transect routes were restricted to areas that were accessible (e.g. footpaths or trails).

To minimize inter-observer variability, only two observers carried out the surveys. We counted birds between 07h00 and 10h00 on days without rain or strong wind. It took 20 min for an observer to survey a transect (average walking speed of 25 m min^{-1}). Birds sighted or heard within 50 m of either side of a transect route were counted. Judgement of distance in field was aided by the use of local maps or range finders (BUSHNELL Yardage Pro). We did not record birds that were flying, unless it was obvious that the flights started or ended within the transects. As the birds were relatively conspicuous (medium to medium-large birds, total body length: 25–43 cm; Robson 2000) and were not shy or cryptic in behaviour, we believed most of the birds within each transect were detected. All transects were visited once in each of six survey periods evenly spaced between 1 February 2000 and 20 February 2001; the two observers each surveyed a given transect three times. We also compared current (this study) and past estimates of bird populations by referring to relevant published and unpublished reports of bird population sizes in Singapore (Gibson-Hill 1952, Hails 1985*a*, *b*; Kang 1989, Ward 1968). If a report only contained density estimates, we multiplied the estimates by a factor (total area of main island divided by transect area) to arrive at approximate population estimates.

Land-use data

To characterize land use, a circle of 250 m radius was centred on each transect. Sampling plots of this extent were chosen so that the effects of local factors on birds could be investigated. Within each circle, we identified plots of land as falling into one of nine defined categories (see Table 1 for a description) through field surveys and consultation with 1:5000 land-use maps obtained from the Urban Redevelopment Authority of Singapore. A plot of

Table 1. A description of the nine land-use categories defined in this study and their respective codes. We defined high-rise as having more than three surface storeys. Each land-use type could also include land uses that were auxiliary to the main use (e.g. car parks as part of PUBLIC). The average proportion (in percentage) of each land-use type and associated standard error were also shown. Proportion of land-use types did not sum up to unity because some land uses were undefined (e.g. roads).

Land use type	Code	Description	Mean % (SE)
1. Public housing	PUBLIC	Government-built high-rise apartments, include apartments with commercial outlets on ground floor; high-rise dormitories	10.1 (3.7)
2. Private apartment	PRIV	Private high-rise apartments; condominiums	4.5 (2.2)
3. House	HOUSE	Low-rise (≤ 3 surface storeys) residential buildings	7.3 (2.2)
4. Commercial	COM	Buildings used for commercial purposes: retail centres, shopping areas, etc.	1.0 (0.3)
5. Industrial	INDUS	Light, general or heavy industries; warehouses; ports, etc.	8.7 (4.0)
6. Urban Green	UGREEN	Managed green open spaces (treed or turfed); urban parks; wayside vegetation; grassy periphery of airport	16.6 (2.9)
7. Institution, community facility and office	INSTIT	Schools; built-up sports facilities; civic and community buildings; army camps; office buildings, etc.	5.5 (2.0)
8. Natural/semi-natural environment	NAT	Unmanaged vegetation; nature parks; unused ground left to regenerate	21.2 (5.2)
9. Agricultural	AGRI	Includes vegetable and animal farms	6.6 (3.9)

land classified under one particular use could contain land uses that were auxiliary to the main one. For example, car parks within public housing estates were classified under PUBLIC. As the bird species were known as human commensals, a classification scheme based on land use might potentially be more meaningful than other types of classification schemes (e.g. natural vegetation types).

Anthropogenic variables, vegetation structure and landscape variables

Within the same circles used for land-use data sampling, we also counted the number of food centres (FOOD). A food centre was defined as a street-level premise that sold cooked food. Birds have free access to these food centres which were potential sources of anthropogenic food through improper food waste handling and disposal. In addition, we defined the percentage of area that was covered by any permanent building, regardless of its intended use, as %BUILT. Immediately following each bird count, each observer surveyed the same transect and counted the number of sites that had exposed edible waste (e.g. food scraps on road). For each transect, we then averaged the data collected over the six surveys (LITTER).

To characterize vegetation along a transect, we first divided each transect into five, 100-m sections. In each section, a circle of 20 m radius was placed randomly on the transect route. The following variables were measured within the circles: number of trees (TREE) (woody plants > 4 m in height, including trees/large shrubs with multiple stems), average height of trees (TR_HT) (four trees at or closest to the four cardinal directions were chosen; if there were less than four trees, all trees were measured) and percentage of ground covered by shrubs (SHRUB) (woody plants with multiple stem ≤ 4 m in height). In addition, we also measured percentage canopy cover (%CANOPY) at the centre of each circle using a spherical densiometer. For each transect, we averaged the measurements obtained from the five circles and used the averages in subsequent analyses. As vegetation sampling was only carried out in a narrow strip (500 × 40 m) in the centre of the transects, it was possible that the vegetation data might not always be representative of the surrounding area. However, this was unavoidable as some transects were bounded by private land.

We also measured the straight-line distance between a transect and the nearest coast (DIST_CST) and human population density (persons km^{-2}) of town planning areas that contained the transects (POP_DEN). Information of the human population density was based on the 1990 national census (Cheng 1995), with each planning area covering between 576 and 2717 ha (equivalent to area of circles with radii between 1.4 and 2.9 km, although the transects were normally not in the centres of the planning areas). With the exception of LITTER, all environmental data were collected only once.

Data analyses

Population estimation To estimate bird population sizes and the associated confidence intervals for each survey period, we first inspected the distributions of the count data. As the distributions did not fit any commonly used distributions (e.g. Poisson or log-normal), we used the non-parametric method of bootstrapping to carry out the estimation (see Efron & Tibshirani 1993). For each species–survey period combination, we re-sampled the count data 1000 times, with replacement, to produce an estimation of the population size. The corresponding 95% confidence intervals were constructed using the bias-corrected and adjusted percentile method (Millard & Neerchal 2001). The average numbers of birds per transect and intervals were then extrapolated to the whole island, based on its total area.

Transformation of bird count data In the regression analyses of individual species, the numbers of birds per transect, averaged over six surveys, were transformed and used as the dependent variables. To achieve normality and homoscedasticity, house crow and common myna abundance data were log-transformed: log (mean abundance + 0.5), while white-vented myna abundance was square-root transformed: (mean abundance + 0.5)$^{0.5}$. P-values of Anderson–Darling normality tests on the transformed variables for the three species were 0.27, 0.17 and 0.37, respectively. Due to the different transformations used for the white-vented myna, results from regression analyses (e.g. regression coefficients) for this species cannot be directly compared with those of the other two.

Principal component regression of land-use variables For each transect, the area of each land-use type was expressed as a proportion of the total area within a circle of 250 m radius. As a result, the land-use data were compositional, as the sum of different land-use types associated with a transect was constrained to one (unit-sum constraint). In reality the data were only approximately compositional, because some land uses (e.g. roads and open water bodies) were not defined. Because the proportions of different land uses were not independent, we did not use the least-squares regression. Instead, we used an alternative – principal component (PC) regression – to calculate the regression coefficient of each type of land use (see Chatterjee *et al.* 2000 for details). When compared to least-squares regression, the estimates of partial regression coefficients derived from PC regression tend to be more stable and have smaller variances if multicollinearities or constraints were present among the predictor variables.

In PC regression, subsets of PCs were selected using Akaike's information criterion (AIC). AIC is based on Kullback–Leibler information and the method of maximum likelihood, and is used to determine the most parsimonious model from a set of a priori candidates, using only the information contained in the empirical data at hand (see Anderson *et al.* 2000, Burnham & Anderson 2001). The subsets of PCs used were contained in the regression models with the lowest AIC_c (AIC corrected for small sample size) scores among a suit of candidate models. Possible candidate models consisted of regression models with PCs removed one at a time based on their t-values, starting from the model with the full set of PCs.

Stepwise regression of anthropogenic variables, vegetation structure and landscape variables We examined the relationships between the dependent variables and the nine non-land-use environmental variables by entering them into forward–backward stepwise regressions (Ryan & Joiner 2001). The t-test P-value for each variable to be entered into and removed from the equation were set at 0.15. As all variables were available for selection, care was taken to detect multicollinearity among the predictors entered in the equations (e.g. we looked for large changes in partial regression coefficients in confirmatory backwards elimination stepwise regression). We also inspected normal probability plots of residuals and plots of fitted values versus residuals, to assess whether the regression assumptions had been violated. Outlier observations with standardized residuals larger than three were removed from the calculations. In addition, we inspected observations (of predictor variables) that had disproportionately large influences on the regressions (i.e. high leverage). The observations with unusual values were detected using h_i (hat matrix diagonal elements, see Montgomery 1997). An observation was considered highly influential if its h exceeded 3p/n where p was the number of habitat variables in the regression equation (inclusive of constant) and n was the total number of observations.

RESULTS

Historical populations

Based on museum skins, the white-vented myna was thought to have first arrived at Singapore around 1920–21 (Figure 2) (Lever 1987). It was followed by the common myna in 1936 and the house crow in 1948 (Gibson-Hill 1952). The two mynas were thought to be plentiful sometime after their colonization, but no quantitative data were available until 1983/84. Hails (1985*a*), using counts conducted in 15 transects (transect size = 10 ha) around the island, estimated that the densities of the white-vented myna and common myna in Singapore were around 315 km^{-2} and 147 km^{-2}, respectively. When extrapolated to the whole of main island, the population sizes of white-vented myna and common myna were approximately 180 000 and 84 000, respectively. Kang (1989) counted the two species in six habitat types using line transects, and estimated the detection radius to be 20–40 m. Assuming that she counted all individuals within 40 m of both sides of

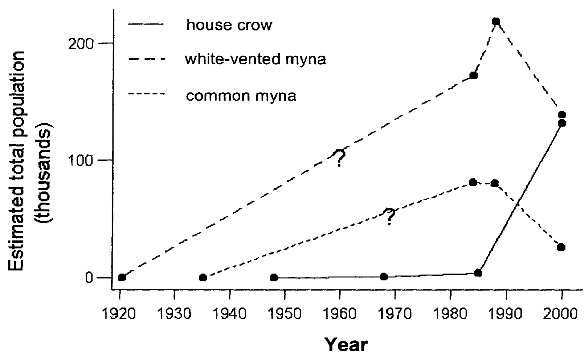

Figure 2. Graph showing estimated total population sizes of house crow, white-vented myna and common myna since their introductions in Singapore. No quantitative data were available for the two mynas before 1983.

Table 2. Estimated population sizes and 95% confidence intervals (in thousands) of house crow, white-vented myna and common myna in Singapore based on an extrapolation of counts in 30 transects. The six transect surveys were carried out between February 2000 and February 2001.

	House crow			White-vented myna			Common myna		
Survey	Population	Confidence limits		Population	Confidence limits		Population	Confidence limits	
period	estimate	Lower	Upper	estimate	Lower	Upper	estimate	Lower	Upper
Feb 2000	176	112	249	148	102	209	27.9	12.7	49.8
Apr 2000	137	91.8	201	134	97.4	194	24.7	10.5	56.8
June 2000	128	85.0	194	155	113	265	20.9	11.0	43.1
Aug 2000	133	83.0	206	122	89.6	188	28.4	17.0	51.8
Oct 2000	106	53.9	190	141	103	190	29.7	16.0	60.7
Jan–Feb 2002	110	70.1	175	135	98.9	185	22.0	13.0	45.9

transects, the densities of white-vented and common mynas were 399 km^{-2} and 146 km^{-2}, respectively (translating to overall population sizes of about 229 000 and 84 000, respectively). Ward (1968) reported that a house crow population of 200–400 had established in 1968 near the site of origin (i.e. sea port). Hails (1985*b*) estimated the total population of the house crow to lie between 1800 and 3700 in 1985.

Current populations and distributions

Both the house crow and white-vented myna numbered no less than 100 000 individuals in any of the survey periods, while the population size of the common myna never exceeded 30 000 (Table 2). Average populations over the six survey periods for house crow, white-vented myna and common myna were 132 000, 139 000 and 26 000, respectively. The relatively large confidence intervals associated with the population estimates were likely to be a result of relatively small sample sizes (n = 30) and high natural variation in number of birds per transect.

Although the house crow and white-vented myna had similar total population sizes, the distribution of the former was more aggregated (see Figure 3). The two sites with most crows (transects E4 and S3, Figure 3) were situated within, or next to, older public housing estates (built in 1975 and 1983), and contained no less than 43.7 crows per transect on average. Conversely, the two sites with the most white-vented mynas were dominated by farms (transect N9) and houses/private apartments (S7). The common mynas were generally low in numbers (mean count < 5.0 per transect) with the exceptions of two sites (N9 and W2), which were both dominated by farms. During all surveys, none of the birds were detected in transect S1 which was situated in primary/tall secondary forest.

Factors affecting distribution

Land use Natural/semi-natural environment (NAT) and urban greenery (UGREEN) were the two most common land-use types when averaged across the 30 sites (Table 1). Urban greenery was found in 90.0% of the sites.

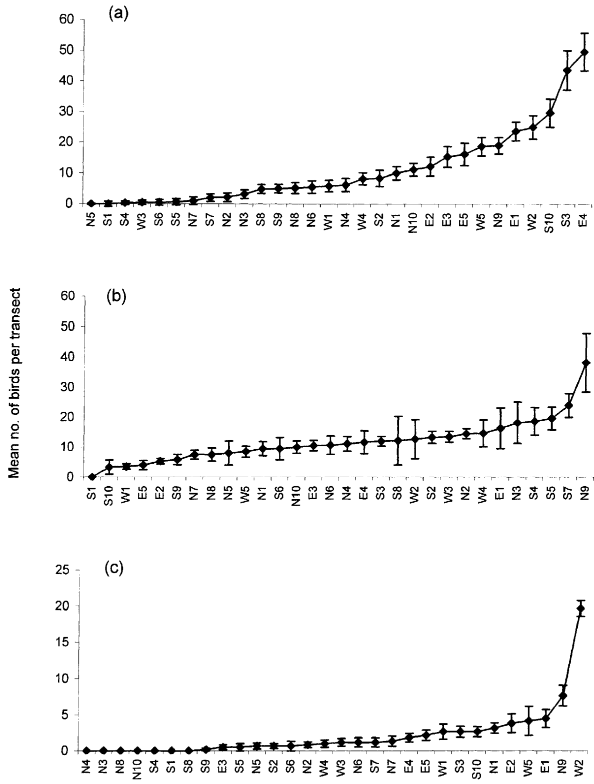

Figure 3. Plots showing mean number of birds per transect (5 ha) arranged in increasing order, for (a) house crow, (b) white-vented myna and (c) common myna. A total of six counts were carried in each transect. The error bars indicate ± 1 SE.

PCA-derived eigenvalues of the nine land-use types showed that land-use patterns could not be adequately summarized by just a few PCs; the first three PCs only accounted for 54.7% of the total variance, while the first five PCs explained 79.0% of the variance. This might be expected, given the relatively small number of strong pairwise correlations between land-use types. Seven out of a total of 36 pairwise Spearman's rank correlations (r_s) had P-values of 0.05 or lower (the value following each pair indicates r_s): PUBLIC-COM, 0.58; PRIV-HOUSE, 0.55; PRIV-INSTIT, 0.51; HOUSE-INDUS, –0.37; HOUSE-INSTIT, 0.42; COM-INSTIT, 0.42; and COM-NAT, –0.50.

Table 3. Partial coefficients of regression between standardized mean abundance of house crow, white-vented myna or common myna and nine land-use types. Partial regression coefficients were derived using principal component regressions (* $P \leq 0.05$).

	House crow				White-vented myna				Common myna			
	Partial coef.	SE	t		Partial coef.	SE	t		Partial coef.	SE	t	
PUBLIC	0.16	0.07	2.14	*	0.01	0.05	0.14		–0.05	0.07	–0.68	
PRIV	–0.12	0.09	–1.39		0.25	0.09	2.60	*	–0.02	0.09	–0.25	
HOUSE	–0.12	0.09	–1.29		0.18	0.09	2.02		–0.02	0.10	–0.26	
COM	0.17	0.08	2.10	*	–0.04	0.03	–1.31		–0.01	0.03	–0.21	
INDUS	–0.01	0.03	–0.46		0.08	0.08	1.06		0.02	0.10	0.23	
UGREEN	0.08	0.04	2.13	*	–0.18	0.09	–1.98		0.01	0.12	0.07	
INSTIT	–0.02	0.04	–0.69		0.01	0.05	0.09		0.06	0.10	0.62	
NAT	–0.04	0.06	–0.57		–0.19	0.08	–2.42	*	–0.29	0.09	–3.25	*
AGRI	–0.02	0.03	–0.43		0.09	0.08	1.06		0.42	0.13	3.33	*

For the house crow, PC regression showed that commercial areas, public housing and urban greenery were significant positive predictors of its abundance (Table 3). Private apartments and natural/semi-natural environment were significant positive and negative predictors of white-vented myna's abundance, respectively. In addition, both houses and urban greenery possessed large positive and negative coefficients, respectively. For the common myna, agricultural land was the most important predictor. Natural/semi-natural environment was also an important land-use type and was found to influence the abundance of common myna negatively.

Anthropogenic variables, vegetation structure and landscape variables Among the non-land-use environmental variables, five pairwise r_s were significant ($P \leq 0.05$), they were: %CANOPY–TREE, 0.45; %CANOPY–TR_HT, 0.45; %BUILT–LITTER, 0.37; POP_DEN–FOOD, 0.41; and %BUILT–FOOD, 0.36.

The best descriptive model for the house crow included number of food centres, distance to coast and litter abundance ($F_{3,26}$ = 11.4, $P < 0.01$) (Table 4). This model explained slightly more than half of the variation in crow abundance. Human population density (range, 0–15 906 persons km^{-2}; mean ± SE, 5468 ± 1052) was initially included in stepwise regression but was later discarded due to its unexpected sign (negative) and its strong correlation with the other two variables in the model (FOOD and LITTER). Entering strongly collineated predictor variables into the same model may cause subsequent statistical inferences of the model to be spurious and is therefore undesirable (Zar 1999). One site had a LITTER value that gave it a large, but acceptable influence (h = 0.60), as it was not substantially higher than the 3p/n value (0.40).

We initially found the best explanatory model for white-vented myna to be a linear equation containing TREE (number of trees) ($F_{1,28}$ = 6.77, P = 0.02). However, the equation included a highly influential site (h = 0.91) and the model was discarded. Automatic curve fitting (searching through linear, polynomial, sigmoidal and exponential curves) with different variables produced a significant ($F_{2,27}$ = 4.48, P = 0.02) quadratic model with CANOPY that contained a moderately high h value (0.48, 3p/n = 0.3). Thus, the white-vented myna was most

Table 4. Results of multiple linear regressions between non-land-use environmental variables and transformed average abundance of each of the invasive bird species.

	Partial regression coefficient	SE	t	P
House crow, log(mean + 0.5)				
Constant	0.82	0.12	6.63	<0.001
FOOD	0.28	0.07	4.08	<0.001
DIST_CST	-1.36×10^{-4}	3.60×10^{-5}	–3.78	0.001
LITTER	0.36	0.20	1.75	0.092
	R^2 = 56.9 %			
White-vented myna, $(\text{mean} + 0.5)^{0.5}$				
Constant	3.16	0.43	7.33	<0.001
%CANOPY	0.040	0.024	1.69	0.103
%CANOPY^2	-6.37×10^{-4}	2.74×10^{-4}	–2.32	0.028
	R^2 = 24.5%			
Common myna, log(mean + 0.5)				
Constant	0.72	0.25	2.93	0.007
TR_HT	–0.035	0.021	–1.68	0.105
SHRUB	–0.014	8.21×10^{-3}	–1.72	0.097
	R^2 = 19.9%			

abundant in transects with intermediate canopy cover (*c.* 35%, averaged across five sampling plots within each transect).

The best explanatory equation for common myna was one containing average height of tree and shrub cover ($F_{2,27}$ = 3.21, P = 0.06), with both variables possessing negative coefficients. Therefore, the common myna probably preferred open terrain with shorter trees and sparser shrub layer. Leverage problem was not severe, with two sites having only moderately high h (0.33 and 0.41, 3p/n = 0.3).

DISCUSSION

Population changes and distributions

We found that the population of the house crow has increased dramatically over the last 16 y, despite active (but moderate) culling of the crows by government authorities since 1973. The number of crows killed in Singapore was several hundreds a year in the beginning of the control programme, but this figure has increased progressively to at least 23 603 in the year 2000 (Sodhi *et al.* 2001). Having occurred in many other parts of the world, the pattern of gradual establishment of house crow followed by explosive growth is certainly not unique to Singapore (see Lever 1987, Long 1981). Between 1968 and 1985, the house crow population in Singapore grew at an average rate of about 15% y^{-1} while from 1985 to 2000, it grew at a much faster rate of 27% y^{-1} (this study). These rates are comparable to that in Mauritius – house crow population grew at a rate of 20% y^{-1} between 1976 and 1988 (Feare & Mungroo 1990), and Kuala Lumpur, Malaysia, – a high 33% y^{-1} between 1970 and 1978 (Davison 1979). By the time of first establishment of house crow in 1969, Kuala Lumpur was already a thriving inland city. The access to large amount of human refuse was one of the likely reasons for such a high rate of growth of crows in this city (Chia 1976).

In Singapore, the slow growth of house crow population in the early years following colonization was what is commonly seen among invasive species, with this period referred to as the 'initial establishment phase' (Mack 1981, Shigesada & Kawasaki 1997). It was possible that the initial invading population of the house crows had low reproductive success due to Allee factors such as difficulty in finding mates (Williamson 1996). As a result, the founding population probably took sometime to disperse to other parts of Singapore. This idea was supported by Ward's (1968) observation that the crows ventured no further than a few hundred yards inland on a stretch of coast (~20 km) around the site of origin before 1966 – 18 y after the first successful colonization.

Due to a lack of long-term quantitative data, it was difficult to determine even the approximate population sizes of the mynas before 1983. However, Ward (1968) mentioned that the common myna was 'the most conspicuous bird everywhere' at that time. Therefore, the common myna might have once been more abundant than the white-vented myna. However, by the early 1980s, the latter was more abundant than the house crow, and was outnumbering the common myna by 2–3 to 1. Hails (1985*a*) felt that this could be attributed to the fact that the white-vented myna was reproducing at a faster rate than the common myna. However, it was equally likely that the common myna had been in decline before the 1980s due to the gradual loss to its preferred habitat – agricultural land.

Although the house crow and white-vented myna have similar overall population sizes, the more aggregated distribution of the former means that it was able to achieve greater local densities. This, combined with the house crow's larger body size and generally more undesirable habits (e.g. constant loud cawing, habit of feeding on rubbish, and its black plumage as a superstitious symbol of bad omens), has made it a much more conspicuous pest bird in Singapore than the white-vented myna.

Habitat associations

One reason why more crows were found in commercial areas might be that they contained more food scraps. Public housing was another land use that was found to be closely associated with house crows in Singapore. Years of public campaigning on cleanliness in Singapore notwithstanding, we still noticed residents throwing food scraps out of windows or leaving them on the ground, presumably to feed animals such as feral cats (*Felis catus*) and birds. In comparison, the amount of food taken by crows directly from waste collection points or spillage during waste handling, though substantial, was generally less (Lim 2002), due probably to the relatively good municipal waste management. Intermediary waste collection points were almost always covered, and the only operational rubbish tip was located offshore. The propensity of the house crow to scavenge was confirmed by the strong explanatory power of the two variables describing the availability of food wastes (FOOD and LITTER). In contrast, we found that the number of food centres was not an important predictor for the abundance of white-vented mynas. This result, however, might be misleading. Wong, S.L.A. (unpubl. data) found that the abundance of white-vented myna and rock pigeons were positively correlated with the size of food centres in Singapore when she counted the number of birds within 15 m of the food centres. Although part of Wong's correlation could be attributed to larger sampling areas in large food centres, her results indicated that the association between white-vented myna and food centre was at a spatial scale not detectable using our sampling technique.

Another unexpected result was that the white-vented myna occurred less often in transects that were surrounded by urban parks. White-vented mynas feed most of the time (> 50%) in short (< 10 cm) grass, capturing preys such as arthropods and annelids (Kang 1989), and therefore one would expect them to find parks or grassed areas suitable habitats. We considered 'stand-alone' parks or managed green areas as UGREEN, but landscaping among apartments or in yards was excluded from this definition (they were considered part of residential development). Therefore, white-vented mynas probably preferred the green patches among residential buildings, as this may have allowed them to more efficiently exploit ephemeral anthropogenic food sources.

Elsewhere in the world, the common myna is known to inhabit open woodland and grassland, and is a common commensal of humans in villages or suburbs (Ali & Ripley 1972, Feare & Craig 1998). It favours ground invertebrates, with fruits and berries constituting a smaller part of their diet (Pell & Tidemann 1997*b*, Sengupta 1982). In Singapore, we found the common myna to be strongly associated with the rural landscape, while its status as the major human commensal sturnid has largely been replaced by the white-vented myna, probably because the latter was more capable of exploiting ephemeral food sources (e.g. mown grass patches, insect swarms, carrion, human refuse). Kang (1989) found that the number of white-vented mynas compared to common mynas at transient food sources exceeded expected population ratios, and the former also visited more transient food sources during radio-tracking.

Landscape variables have previously been used to improve the descriptive ability of models containing local habitat variables, and have been shown to correlate significantly with bird abundance (e.g. Bolger *et al.* 1997, Germaine *et al.* 1998). We found, contrary to our a priori expectations, that the three invasive species we studied were probably not directly affected by human population density in the surrounding areas. There were few possible reasons for the lack of significance of POP_DEN in describing bird abundance. The census data of human population density might not necessarily reflect what was the density at the time of bird counting due to large intraday movement of people for reasons such as work. Substantial changes might also have occurred since the 1990 census, but relevant data from the latest census conducted in year 2000 were not yet available. Another reason could be that Singapore was so well urbanized that there were few variations in the amount of urbanization at a landscape level. Thus, the birds were responding more to local factors.

Overall, we found that land-use data alone were not very good descriptors of the abundance of the three species. The two or three most predictive PCs for each of the species explained less than a quarter of the variation in bird abundance (R^2 = 16.5–24.4%). However, the lack of effect of %BUILT in the stepwise regressions suggested that differing cultural usage of the land was more important than the mere presence of buildings and humans. On the other hand, non-land-use variables described slightly more than half of the variation in crow abundance (but the descriptive abilities of the non-land-use variables were poorer for the mynas). In bird–habitat relationship studies, uncertainties in model structure and parameter estimates are not uncommon, and can be caused by a number of factors, such as random or unpredicted fluctuations in the environment or lack of precise knowledge of birds or habitats (e.g. our inability to measure vegetation beyond a central strip) (Gutzwiller & Barrow 2001).

Due to their negative impacts on the environment and economy, invasive species eradication is a key focus for managers. However, the success of such management efforts may hinge on the ecological understanding of the species and its interactions with the environment. Our study shows that three invasive bird species in Singapore associated with different aspects of the human-modified environment. Therefore, 'across-the-board' management actions may not be effective for all pest bird species in an urban area. Further, there may be interactions among the invasive species and management for one species may result in the higher abundance of another (Yap *et al.* 2002).

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