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SPACE USE AND HABITAT SELECTION OF HOUSE CROWS IN A TROPICAL URBAN ENVIRONMENT: A RADIO-TRACKING STUDY

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ABSTRACT. – The house crow (*Corvus splendens*) is an invasive bird in many parts of Asia. A radio-tracking study was conducted on 13 randomly selected birds caught throughout the port city of Singapore. We found that house crows returned faithfully to specific daytime areas and roost sites. Home range (95% fixed kernel utilization distribution [UD]) size ranged from 1.3 to 158.1 ha while core area (50% UD) size ranged from 0.2 to 22.3 ha. Crows that have formed pair bonds remained in their core areas for longer each day, and possessed smaller home ranges and core areas compared to other birds. In the middle part of the day, house crows remained in their core areas where the bulk of feeding occurred. In addition, they used supplementary feeding sites, which coincided with afternoon gathering points. House crows in Singapore travelled only short distances (maximum = 3.5 km) to their roost sites, unlike house crows studied elsewhere. Habitat selection analyses carried out at two spatial scales showed that house crows preferred commercial and public housing land uses, corroborating results from a count-based study. This was probably due to the higher amount of anthropogenic food found in these places. By understanding the crows' movement patterns and habitat preferences, management practices can be more focused and successful.

KEY WORDS. – Anthropogenic food, invasive species, wildlife management, radio-telemetry, urban ecology.

INTRODUCTION

The house crow (*Corvus splendens*), though originally from a geographic region stretching from southern Iran to Thailand, has successfully spread to many towns and cities surrounding the Indian Ocean (Meininger et al*.*, 1980; Long, 1981). It is a highly gregarious species that has survived alongside humans by scavenging and generally relying on a versatile diet (Madge & Burn, 1994). Its invasions have attracted attention of wildlife managers because of the bird's well documented negative impact on native wildlife, agricultural crops, and—by harboring of pathogens that cause enteric disorders—even human health (Jennings, 1992; Ryall, 1992; Archer, 2001).

House crows probably invaded Singapore during the 1940s as stowaways on ships (Gibson-Hill, 1952). Having established a population of 200–400 in a port area by 1968 (Ward, 1968), they experienced explosive growth in 1980s and 1990s, with population size reaching about 132,000 in 2000 and local densities as high as about 9 birds/ha (Lim et al., 2003). This high density, combined with its raucous nature and a tendency to form large, noisy and polluting colonial roosts near residential areas, led to the desire to control the population in Singapore (Hails, 1985). To develop effective management strategies for the species, several studies have been carried out in Singapore to shed light on the following aspects of their ecology: roosting behavior and roost site selection (Peh, 2002; Peh & Sodhi, 2002), nest site selection (Soh et al., 2002), and their habitat-abundance relationship (Lim et al., 2003). Knowledge gleaned from these studies formed the basis of an eradication program that aimed to cut crow population in Singapore by about 90% (Brook et al., 2003).

The purpose of this paper is to report on a further study of house crows in Singapore, specifically their use of space and habitats. Whether the crows are faithful to particular daytime areas and nocturnal roost sites is unknown, as is whether the crows use one area during the course of a day, or are there multiple sites of concentrated activity. In particular, the aims of this study are to: (1) document home range and diurnal movement patterns; (2) study food selection, and evaluate if use of sites coincide with feeding activities; and (3) test if the use of habitat types occurs in proportion to availability. Finally, we recommended management strategies for effective and efficient control of house crows based on our findings.

MATERIAL AND METHODS

Study Area. **–** Singapore (1°20'N 103°50'E), is a densely populated tropical island-state with more than four million people in an area of about 700 km^2 (Singapore Department of Statistics, 2007). Most of the original vegetation (mainly lowland tropical rainforest) has been lost to development, and only about 1,700 ha remains (Corlett, 1992). Farmland covers a small proportion of the total land area (746 ha; Agri-Food and Veterinary Authority of Singapore 2007). As much as 50% of the land is considered built-up, but is often interspersed with an assortment of managed green spaces, urban parks and wayside vegetation (Corlett, 1992).

Trapping and radio-tracking. **–** To capture house crows, we divided the main island of Singapore into 2 km^2 grid cells and visited them at random. At each site, we attempted to capture crows for up to four days. We caught most crows by sedation with buttered bread cubes (1 cm^3) laced with 0.02g of 10% alpha-chloralose (Stouffer & Caccamise, 1991a). Each crow was held in captivity overnight and then fitted with a 4.9g radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota) the next day. The transmitter was attached to one of the two central rectrices with its antenna extending beyond the feather. The weight of a transmitter was less than 2% of the average mass (± SE) of the crows trapped (251.5 ± 6.4g). Each radio-tracked crow was also fitted with colored plastic leg bands. We assigned crows to the following age categories based on the methods of Davison (1979): juvenile (< 6 months), immature (6–18 months) and adult (> 18 months). Sexing of birds was not carried out because sexes were not distinguishable based on plumage.

Each crow was radio-tracked for 4–5 days per week until the transmitter failed or when home range size did not increase substantially with increasing number of radio-locations. We attempted to obtain three radio-locations separated by at least 30 min each day a bird was followed. The radio-locations of a crow collected within the same day were autocorrelated (Swihart & Slade, 1985). However, we felt that this was not important because in the subsequent habitat selection analyses, we used the animals' home ranges and not individual radio-locations as the sampling units (Otis & White, 1999). Further, use of completely independent radio-locations is also not necessary when estimating home ranges using the kernel method adopted here (Swihart & Slade, 1997). To ensure unbiased sampling of the daylight period (approximately 06:30–19:30 hr, inclusive of twilight), we separated time into one-hour blocks and attempted to obtain similar number of radio-locations within each time block. House crows were not active in the evening as they congregated in communal roosts. Up to three crows were tracked simultaneously.

We located birds on foot using a receiver (LA12-Q, AVM Instruments, Colfax, California) with a hand-held four-element Yagi antenna. When a signal could not be detected, we attempted to find the bird by driving in a vehicle with a roof-mounted omni-directional antenna. Three levels of accuracy could be ascribed to the radio-locations obtained with the Yagi antenna: direct sighting and identification of bird (type I, most accurate); triangulation within a short (approximately ≤ 30 m) distance (type II, sometimes a group of crows was sighted but the radio-tracked bird was not identified); triangulation from more than 30 m away (type III). For triangulation from more than 30 m, two bearings were taken no more than 10 min apart to minimize the chance of bird movement. Because the antenna was field tested before actual tracking, error polygon sizes could be calculated. The error polygon size of type II radio-locations are not given because they are generally very small. We retained most type III locations because it is more problematic to introduce systematic errors by routinely censoring some locations (e.g. those from the more inaccessible parts of the home ranges) than to introduce imprecision by including radio-locations with larger error polygons (Nams, 1989). We plotted all radio-locations and bearing locations on 1:7500 maps before transferring them to the computer.

When the behavior of a radio-tracked crow could be observed (type I locations) or inferred (type II locations), we noted whether the bird was foraging (consuming, handling, or acquiring food), and the type of food being consumed. Other activities of the crows were not recorded because the resources involved might not have been limiting (e.g. perch sites) or were tied to certain habitat types.

Home range, habitat selection and foraging. **–** We used the fixed kernel method to estimate home ranges (Worton, 1989). Calculations were carried out using Animal Movement (Hooge & Eichenlaub, 2000), a program extension of ArcView software (ESRI, Redlands, California). The least-square cross validation method was used to find the optimal smoothing parameter (Silverman, 1986). Home range and core area of a bird were defined as the 95% and 50% utilization distributions (UDs), respectively. Error polygons were plotted in the GIS environment using the program LOAS (Ecological Software Solutions, Sacromento, California).

For analysis of habitat selection, we compared available and used habitats at two spatial scales: study area (i.e. Singapore main island) versus home range (landscape level), and home range versus core area (home range level). These levels of selection corresponded to Johnson's (1980) second-order selection (i.e. of home ranges) and third-order selection (of habitat components within home ranges), respectively. At the landscape level, availability of habitats was estimated by placing 30 randomly-placed circular plots in Singapore (radius = 250 m, see Lim et al., 2003 for more details).

Table 1. Description of land use categories. Each type includes land uses that are auxiliary to the main use (e.g. parking lots as part of PUBLIC).

Land use type	Code	Descriptions
Public housing	PUBLIC	Public high-rise apartments, includes apartments with commercial outlets on ground floor; high-rise dormitories
Private apartment	PRIV	Private high-rise apartments; condominiums
House	HOUSE	Low-rise ($\leq$ 3 surface storey) residential buildings
Commercial	COM	Buildings used for commercial purposes; retail centers; shopping areas
Industrial	INDUS	Light, general or heavy industries; warehouses; ports
Urban green	UGREEN	Managed green open spaces (treed or turfed); urban parks; wayside vegetation
Institution, community facility and office	INSTIT	Schools; built-up sports facilities; civic and community buildings; army camps; office buildings
Natural/semi-natural environment	NAT	Unmanaged vegetation; nature parks; unused ground left to regenerate
Agricultural	AGRI	Vegetable and animal farms

Used habitats were those found within the home ranges (area bounded by 95% UDs). At the home range level of selection, used habitats were those within the core areas (50% UDs), whereas available habitats were those within the home ranges. We studied habitat selection using UDs because this approach treated individual animals as the sampling units and defined use probabilistically based on overall movement patterns (Millspaugh et al., 2006).

Nine habitat types were defined based on anthropogenic land uses (Table 1). Other definitions of habitat types (e.g. natural habitats based on vegetation type) were not employed because house crows in Singapore occur mainly in areas influenced heavily by humans. At the landscape level, we compared the proportion of land use types in the circular plots and home ranges using Mann-Whitney *U*-tests, one category at a time, to determine if house crows preferred certain land use types when it comes to selecting their home ranges. Compositional analysis (Aebischer et al., 1993) was used to analyze habitat selection at the home range level because it overcomes the problem of non-independence of habitat proportions via log-ratio transformation (Aitchison, 1986). We calculated all possible pairwise differences in log-ratios between used and available habitats (i.e. $\ln[x_{ui}/x_{ai}] - \ln[x_{uj}/x_{aj}]$, where x_u is an individual's proportional habitat use, x_a is an individual's proportional habitat availability, $i = 1, 2\ldots, p$ and $i \neq j$ given p habitat types; Aebischer et al., 1993), and then averaged the matrices across all individuals. Significant departure of means from zero were tested using *t*-tests (mean/standard error), and a positive value signified that row land use type was preferred over the corresponding column land use type (see Results). To rank habitat types in order of preference, the number of positive values across a row was summed. Habitat types with more positive values were more preferred. All following values are presented as mean ± SE.

RESULTS

Home range, movements and food selection. – We tracked 13 crows (N = 8 adults, 3 immatures, and 2 juveniles) for an average of 21.2 ± 0.9 days, and obtained an average of 35.6 ± 3.0 radio-locations per bird (Table 2). The proportion of radio-locations per bird derived through direct sightings (type I radio-locations) ranged from 19.2–75.0% (mean = 45.2 ± 5.2%). The average size of 95% error polygons from

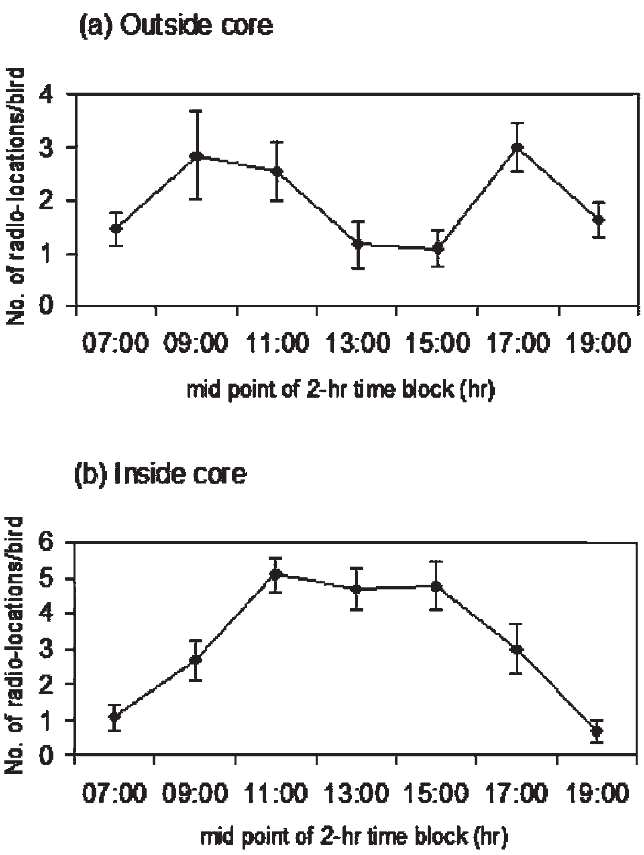

Fig. 1. Average number of radio-locations per bird (a) outside or (b) inside core areas within each 2-hr time block. Number of House Crows = 13. Labels on x-axis indicate midpoint of each time block. Error bars denote standard errors.

Table 2. Size of home ranges and core areas (defined by the fixed kernel method) and other information on 13 House Crows radio-tracked between 13 May 2000 and 8 Feb.2002.

Bird	Age[1]	No. of days tracked	No. of radio-locations	Home range (ha)	Core area (ha)	MCP[2] (ha) (ha)	Approx. distance from roost(s) to core area(s) (km)
51	I	17	21	82.3	15.7	37.9	0.90
62	A (P)	16	23	1.3	0.2	1.2	1.67
130	A	24	46	44.6	9.0	92.5	1.78
157	A	44	60	19.4	2.3	34.3	3.50
166	I	18	20	32.3	3.6	28.7	1.53
182	A (P)	23	33	9.4	3.1	15.0	1.17
183	A (P)	23	43	2.4	0.5	14.7	0.87
271	J	23	40	9.8	2.0	6.4	2.32
293	A	26	37	62.2	7.8	175.3	2.86
389	A	22	34	130.5	22.3	425.4	3.42
424	I	25	35	84.8	11.8	178.6	1.01
565	A	25	36	158.1	14.5	212.4	1.27
630	J	18	35	9.5	0.9	8.9	0.51

[1] A = adult, I = immature, J = juvenile and P = pair-bonded
[2] MCP = minimum convex polygon

type III radio-locations was 5.0 ± 1.2 ha (N = 40). Three adults formed pair bonds (displayed affiliative behavior; Brown & Veltman, 1987), but did not nest (lay eggs, incubate or brood).

Home range sizes ranged from 1.3 ha to 158.1 ha. Paired adults had smaller home ranges (mean = 4.4 ± 2.5 ha) and core areas (mean = 1.3 ± 0.9 ha) than the other crows (mean home range size = 63.4 ± 14.6 ha; mean core area size = 9.0 ± 2.0 ha). Between paired adults and other crows, differences in size of core areas and home ranges were both statistically significant (Mann-Whitney U-test, core area: P = 0.049, home range: P = 0.007). The mean distance between approximate centers of core areas and roost sites was 1.8 ± 0.3 km (N = 13). Crows tended to remain in their respective core areas in the middle part of the day, but were found outside the core areas during early morning and late afternoon (Fig. 1). Daily afternoon departures from core areas to roost sites occurred later for paired crows than for unpaired crows. The latest a paired crow was detected at the core area was, on average, 18:36 hr (range: 18:10–19:02 hr, N = 3), whereas the latest time for unpaired birds was 16:30 hr (range: 14:04–18:45 hr, N = 10). Six of 13 crows had at least one substantially-utilized home range portion (≥ 8% of the bird's total number of radio-locations) that was discontinuous from the core area (based on fixed kernel definition of home range configuration). Throughout our study, only two birds switched roost. One bird moved to an existing roost 1.25 km away because its original roost was subjected to shooting. Another bird switched to an alternative roost 400 m away even though the first was not subjected to any apparent disturbance.

Overall, 44 radio-locations (10.4% of type I and II radio-locations) were associated with foraging. Most feeding occurred in the core areas, with another peak during late afternoons (Fig. 2). Although 73% of feeding occurred within core areas, χ^2 tests indicated that this proportion was not significant (P = 0.36, d.f. = 1) because more type I and II locations also fell in core areas (67%). However, we felt that this lack of statistical significance was an artifact of how the crows were radio-tracked. They generally moved faster during the early morning and late afternoon (moving away or towards their roosts), and were consequently harder to sight. Therefore, even if the crows did not forage often outside of their core areas, observations relating to this were difficult to collect.

Food of 'natural' origin (not directly derived from humans) accounted for 20.5% of the total observed. These food items included beach and canal bank debris, insects, and fruits on trees. The crows used a variety of feeding techniques such as gleaning off beaches, ground or other substrates, probing tree bark, and flycatching. The largest proportion of food was litter or food offered deliberately to crows or other

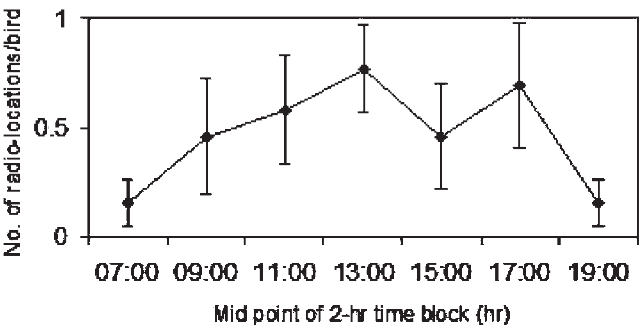

Fig. 2. Average number of radio-locations per bird associated with feeding within each 2-hr time block. Number of House Crows = 13. Labels on x-axis indicate mid point of each time block. Error bars denote standard errors.

Table 3. Comparison of the proportion of land use types in 30 random plots located in Singapore and those within home ranges (95% fixed kernel utilization distribution) of 13 crows. AGRI (agricultural land uses) was excluded from the analysis because none of the home ranges contained this land use type.

Land use type	Random plots (%) Mean (SE)	Home ranges (%) Mean (SE)
PUBLIC	10.1 (3.7)	27.8 (6.9)**
PRIV	4.5 (2.2)	1.3 (0.7)
HOUSE	7.3 (2.2)	16.9 (7.3)
COM	1.0 (0.3)	2.8 (1.0)*
INDUS	8.7 (4.0)	14.2 (5.7)
UGREEN	16.6 (2.9)	19.6 (5.3)
INSTIT	5.5 (2.0)	11.6 (3.3)**
NAT	21.2 (5.2)	6.0 (2.3)
AGRI	6.6 (3.9)	–

** Mann-Whitney U test, significantly different at $P = 0.05$; * significantly different at $P = 0.10$

animals (e.g. Rock Pigeons *Columbus livia*) (55.0%). Due to good municipal practices, a relatively small proportion (8.5%) came directly from waste disposal sites or spillage. The remaining food items were of uncertain origin. The small number of feeding observations precluded detailed analyses on individual birds (e.g. relative proportions of each type of food) but the data and locations of core areas suggested that individual birds vary in their reliance on natural food.

Habitat selection. **–** Proportions of the two land use types differed significantly within the study area and the home ranges (Mann-Whitney *U*-test, $P = 0.05$) (Table 3). Home ranges contained a significantly greater proportion of PUBLIC and INSTIT. Home ranges also had larger proportions of COM compared to the study area, but this was significant only at $P = 0.10$. Crows appeared to avoid areas with natural vegetation and private apartments, although the relationships were not statistically significant (Table 3). AGRI was excluded from the analysis because none of the home ranges contained this land use type.

Multivariate analysis showed overall departure from random use when land use compositions of core areas and home ranges were compared (Wilks' $\Lambda = 0.3$, $P < 0.05$ when compared to χ^2_7). The ranking of preference (descending order) based on the number of positive mean log-ratio differences in each row is: PUBLIC > COM > INDUS > PRIVATE > UGREEN > NAT > INSTIT > HOUSE (Table 4). Some lack of congruence within this dataset was noticeable. For instance, although COM was significantly preferred over INDUS ($P = 0.04$), the *t*-test did not show that PUBLIC was significantly preferred to INDUS, even though PUBLIC was ranked higher than COM. Therefore, the final ranking of habitat preference should be viewed as a general ranking that shows the average preference of a sample of crows.

PUBLIC was the largest component (41.2–97.4%) in the core areas for six of the crows. Three other crows had UGREEN as the major component (53.0–90.4%). The largest core area components of the other four crows were INDUS (95.3%), INSTIT (63.8%) and HOUSE (81.8% and 100.0%). For two land use types, COM and PUBLIC, use by house crows increased linearly with availability at the home range level (Fig. 3). Although there are positively significant relationships between use and availability for some of the other land use types, those regressions were affected by high leverage values (i.e. one or a few points having unduly large influence on the regression; Montgomery, 1997).

DISCUSSION

Home ranges and movements. **–** House crows are a community-territorial species, which form loose nesting colonies and benefit from close association with each other through the collective defence of nests and mobbing of predators (Lamba, 1963; Rowley, 1973; Soh et al., 2002). Despite the difference in social organization, home range sizes of house crows in Singapore are comparable to those of similarly-sized *Corvus* species that defend territories.

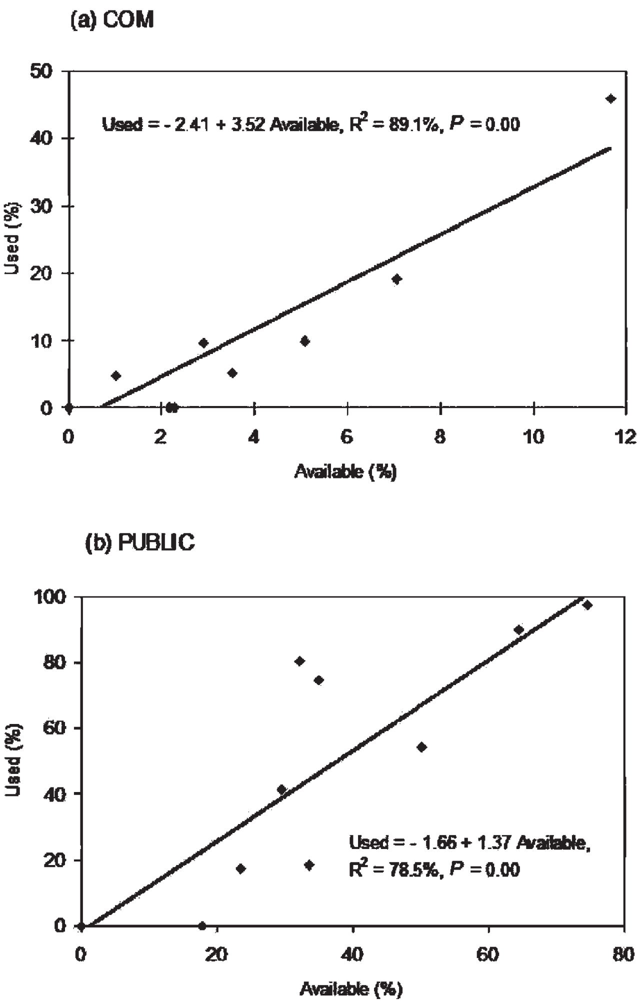

Fig. 3. The proportions of (a) commercial and (b) public housing land uses in core areas (y-axis) against proportions in home ranges (x-axis) for 13 House Crows.

Table 4. Matrix of means and standard errors of differences in log-ratios calculated from use/availability (core area/home range) data of 13 House crows. A positive matrix element signifies that the row land use type is preferred over the column land use type. Means are tested for significant differences from zero using *t*-test (in bold, significant at $P = 0.05$). The rank on the right is the sum of the number of positive values in the row.

	PUBLIC	PRIV	HOUSE	COM	INDUS	UGREEN	INSTIT	NAT	Rank
PUBLIC		2.09 ± 1.15	**3.46 ± 1.39**	0.97 ± 1.31	1.97 ± 1.57	2.62 ± 1.27	**3.03 ± 1.08**	**2.78 ± 1.13**	7
PRIV	-2.09 ± 1.15		1.37 ± 1.12	-1.99 ± 1.47	-0.12 ± 1.76	0.69 ± 1.38	0.95 ± 1.22	0.69 ± 1.38	4
HOUSE	**-3.46 ± 1.39**	-1.37 ± 1.12		-3.37 ± 1.61	-1.49 ± 1.81	-0.84 ± 1.32	-0.43 ± 1.48	-0.68 ± 1.00	0
COM	-0.97 ± 1.31	1.99 ± 1.47	3.37 ± 1.61		**1.87 ± 0.79**	2.53 ± 1.80	2.94 ± 1.43	2.68 ± 1.48	6
INDUS	-1.97 ± 1.57	0.12 ± 1.76	1.49 ± 1.81	**-1.87 ± 0.79**		0.65 ± 2.03	1.06 ± 1.79	0.81 ± 1.67	5
UGREEN	-2.62 ± 1.27	-0.69 ± 1.38	0.84 ± 1.32	-2.53 ± 1.80	-0.65 ± 2.03		0.41 ± 1.49	0.16 ± 0.95	3
INSTIT	**-3.03 ± 1.08**	-0.95 ± 1.22	0.43 ± 1.48	-2.94 ± 1.43	-1.06 ± 1.79	-0.41 ± 1.49		0.25 ± 1.57	1
NAT	**-2.78 ± 1.13**	-0.69 ± 1.38	0.68 ± 1.00	-2.68 ± 1.48	-0.81 ± 1.67	-0.16 ± 0.95	0.25 ± 1.57		2

Minimum convex polygon home range sizes of some of the other *Corvus* species that have been studied are: American crow, with a 26–49 ha group territory (Stouffer and Caccamise 1991b); carrion crow (*C. corone*), 22–29 ha (Nakamura 1998); Torresian crow (*C. orru*), 131 ha (average), and Australian Raven (*C. coronoides*), 109 ha (average) (Rowley, 1973). However, because house crows only defend nests or nest trees, and not territories, they can achieve much higher local densities if sufficient resources are available. Crowding of high quality sites has also been observed in American crows, albeit to a lesser extent, where their territories of overlap in food-rich areas (Marzluff & Neatherlin, 2006). Paired adult house crows possessed significantly smaller activity areas in contrast to birds that did not form pair bonds. This suggests that they either established themselves in higher quality sites, or that they were more dominant when competing for temporarily abundant food within their home ranges.

The crows we radio-tracked travelled short distances to roost (maximum = 3.5 km). Other studies on house crows reported distances of 8.5 km in Kuala Lumpur, Malaysia (Chia, 1976) and 25 km in Mauritius (Feare & Mungroo, 1990). Difference in study design may partially account for these travel differences. These earlier studies had only a single roost in their study areas, allowing the detection of maximum travel distances. However, we believe two other factors may also contribute to the shorter distances travelled by house crows in Singapore. First, the high density of crows in Singapore (Lim et al., 2003) permits a relatively small area to provide an adequate number of birds for communal roost formation. The smallest roost in Singapore detected by Peh (2002) contained about 50 birds. Second, there is no shortage of suitable roost trees in Singapore because of an intensive urban greening program (> 1 million trees planted in parks and roadsides; Anonymous, 2003). Thus, if roosts are just passive aggregations of birds (Caccamise et al., 1997), and suitable roost trees are not limiting, we should expect roosts to be located such that they minimize travelling cost to daytime centers.

Although core areas may be responsible for the bulk of the food intake, our study shows an interesting secondary peak in feeding, at a time when crows have moved out of their core areas. We found that such supplementary feeding often occurred at convergence sites which the crows visited before proceeding to the vicinity of roosts for pre-roosting. Chia (1976) also documented the presence of such late afternoon convergence sites (termed post-feeding assembly points), but he did not explicitly determine if supplementary feeding was carried out. The use of supplementary feeding sites at varying distances from territories by American crows has also been documented (Stouffer & Caccamise, 1991b; Caccamise et al., 1997). Because of the lack of seasonality in food abundance in Singapore, such supplementary feeding sites may be less important to house crows than they would be for temperate corvid species.

We found that the birds in Singapore returned to their core areas faithfully, even though they roost communally. This behavior has been reported for other communally roosting species as well, e.g. common grackle (*Quiscalus quiscula*) (Caccamise et al., 1983); European starling (*Sturnus vulgaris*) (Morrison & Caccamise, 1985); common myna (*Acridotheres tristis*) and Javan myna (*A. javanicus*) (Kang, 1989). Tangentially, we note that our findings of fidelity to such daytime centers, and the observation that the majority of feeding was carried out within core areas, are inconsistent with the information center hypothesis of communal roosting behavior (Ward & Zahavi, 1973), which generally predicts a roost-centered distribution of foraging sites. This pattern is expected because the hypothesis posits that birds exchange information at their roost sites, resulting in naïve birds following knowledgeable roost-mates to profitable feeding sites. Despite this apparent lack of support for the hypothesis, we acknowledge that house crows in Singapore may not represent a strong case against the information center hypothesis. This is because food resources in Singapore may not be temporally and spatially ephemeral enough, such that crows need to follow knowledgeable roost-mates in order to feed successfully (Sonerud et al., 2001). Studies in places where food occurrence is more sporadic (e.g. coast) at the day-to-day time scale are needed to test if house crows indeed use roosts for information exchange (Tye, 1993).

***Habitat selection.* –** Our radio-tracking study agrees with a count-based study (Lim et al., 2003) in indicating that house crows in Singapore prefer public housing and commercial areas. Both this and the count-based study show that crows were attracted to these land uses because of the high amount of anthropogenic food. The two studies, however, disagree on house crows' preference for institutional land uses (they were found to be negative predictors of crow abundance in the count-based study). We believe the cause of the discrepancy lies in how home ranges were derived. Mathematically constructed home ranges, which are partially based on spatial extrapolation from actual radio-locations, may sometimes include less preferred sites (i.e. institutes) because they intermix with or are embedded within more preferred ones (e.g. schools adjacent to public housing). However, at the home range level of analysis, institutional use sites were strongly avoided, thus showing that, overall, they are indeed not favored.

We believe that frequently used habitats are of better quality by virtue of their more abundant food resources. There is evidence that the existence of extra food caused increased fecundity and survival in other species of crows (Richner, 1992; Marzluff & Neatherlin, 2006). Even if survival or reproductive success of individual crows did not improve because of increased crowdedness in preferred habitats, density, which is an important indicator of habitat quality (Van Horne, 1983), was clearly elevated in food-rich habitat types. Direct evidence for this was found by Lim et al.'s (2003) count-based study. Moreover, we provided indirect evidence here by showing that use of commercial and public housing areas increased linearly with their availability. If crows only need to extract a fixed amount of resources (i.e. food) from commercial or public housing areas, the use of these areas should plateau after the birds' needs are met (Garshelis, 2000). This will not be the case if more available habitat also attracts more birds, forcing individuals to increase use of commercial or public land uses in order to maintain the same intake level.

***Management implications.* –** This study shows that management efforts (e.g. shooting, food limitation) are most profitable when they are carried out in habitats that make up the crows' core areas. Areas occupied by potential breeders or paired crows may be of particularly high quality since these birds can be sustained by rather small habitat area. These sites can usually be identified by presence of active or used nests. By reducing the attractiveness of these habitats through food limitation and access denial (e.g. through frequent shooting, placement of scaring devices), crows would be forced to use lower-quality or less familiar habitats. In contrast, management actions that focus on roost sites are less likely to be effective because birds can change roosts without much apparent cost; studies from elsewhere have shown that crows can cover much longer distances in their daily flights between roosts and daytime sites.

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