

# What facilitates urban colonisation by Crested Pigeons *Ocyphaps lophotes*?

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The Crested Pigeon's *Ocyphaps lophotes* range expansion in south-east Australia has encompassed urban areas, but its urban ecology is insufficiently known to allow identification of factors facilitating urban colonisation. In 2008, we documented its autumn/winter habitat use and foraging ecology and that of potentially competing Feral Pigeons *Columba livia* and Spotted Turtle-Doves *Streptopelia chinensis* in Melbourne. Crested Pigeons occupied three of the five urban habitats surveyed, but particularly occurred in open parkland where most of their foraging took place. Turtle-Doves were ubiquitous, but foraged mostly in streetscapes. Feral Pigeons occupied all habitats except bushland, but their density did not vary among habitats. Foraging substrate use, foraging behaviour and probably the seed diet of all three species were very similar. Crested and Feral Pigeons always foraged within five metres of con-specifics and Spotted Turtle-Doves did so on 84 per cent of occasions. Each species also foraged with at least one of the other pigeon species, but infrequently ( $\leq 14\%$  of records for any species). Intra- and inter-specific aggression was rare among pigeons foraging in close proximity. Factors possibly facilitating Crested Pigeons' residence in Melbourne in autumn and winter include: (a) an evolutionary history in open woodland and savanna, equipping them to exploit urban open parkland, (b) the high abundance of grass and herb seeds (c) the lack of aggressive competition for food with other pigeons and (d) limited ecological isolation from Spotted Turtle-Doves through partly different habitat use.

## INTRODUCTION

Urbanisation causes some of the greatest local extinction rates and frequently eliminates most native species (McKinney 2002). Its rapid spread and the concentration of human populations in cities (Bridgman *et al.* 1995) makes it important to discover how to successfully preserve native wildlife in cities for several reasons, including its aesthetic and educational values, its positive effects on human health and psychological wellbeing and the conservation of local biodiversity (Savard *et al.* 2000; Platt and Lill 2006; Dearborn and Kark 2010).

Urban environments provide suitable habitat for only a limited subset of the regional, native bird species, many of which colonise suburbia soon after it has been constructed and the vegetation is established (Green 1984; Parsons *et al.* 2006). A further wave of avian urban colonisation has occurred in Australia recently, involving several native species of varying ecology which have occupied long-established suburbs in many towns and cities at relatively high densities, either seasonally or permanently (Low 2002). As in other countries, these colonising events are often part of a more general range expansion and population increase resulting from anthropogenic habitat alteration (Garrott *et al.* 1993) and they can potentially cause many of the same negative impacts on suites of other locally indigenous bird species and human economies as those attributable to exotic invaders. Thus in eastern Australia, Pied Currawongs *Strepera graculina*, Noisy Miners *Manorina melanocephala* and Australian White Ibis *Threskiornis molucca* have relatively recently become established in cities and negatively affect many other co-habiting native bird species and human residents through their predatory habits, competitive

behaviour or environmental 'pollution' (Major *et al.* 1996; Catterall 2004; Martin *et al.* 2007). However, there are also some recent native bird colonisers whose presence in cities may, on balance, be considered largely beneficial (Lowry and Lill 2007). To manage urban colonisation by native birds optimally, we need to understand what has caused these recent colonisation events, identify the factors in the urban environment facilitating them and evaluate the costs and benefits involved. Research with this focus could help planners to better integrate the needs of 'desirable' native birds into the design of urban areas.

The abundance of the Crested Pigeon *Ocyphaps lophotes*, a ground-forager originally restricted to dry open woodland, savanna and scrubland in arid and semi-arid mainland Australia (Olsen *et al.* 2006), has increased due to pastoral activities and its range has been expanding towards the south-east coast since at least the 1930s (Higgins and Davies 1996). Crested Pigeons have an inherent ability to exploit anthropogenically-disturbed areas, such as burned woodland and land cleared for agriculture (Frith *et al.* 1974; Kutt and Woinarski 2007), which provide the grass and herb seeds and leaves that dominate their diet (Frith *et al.* 1974). During the species' range expansion, it has colonised many towns and cities in coastal south-east Australia, where it reportedly occupies streets, parkland, golf courses and sports grounds (Higgins and Davies 1996). Its abundance increased dramatically from about 1991 onwards in Canberra (Veerman 2002), where it spread from northern and central to southern parts of the city in six years. It first colonised Adelaide in the 1950s and its population density in the city is now twice that in rural woodland further north in South Australia (Johnston 2006). The Crested Pigeon's occurrence in suburban gardens in Brisbane increased by 34 per cent from 1979 to 1999 (Woodall

2002) and in Melbourne its range is currently rapidly expanding into the eastern suburbs (AL, pers. obs.). However, many aspects of its biology have not been documented in detail (Higgins and Davies 1996) and its urban ecology is not well known.

Melbourne and some other southern Australian cities are also inhabited by two exotic pigeons, with apparently similar foraging ecology to that of the Crested Pigeon, which could potentially influence urban colonisation by this species. Spotted Turtle-Doves *Streptopelia chinensis* inhabit cultivated land, gardens and settlements in their natural range in Asia (del Hoyo *et al.* 2004). They were introduced to Victoria in the 1860s–1870s through deliberate releases in Melbourne and are now established in eastern, southern and south-western Australia and very common in towns and cities (Higgins and Davies 1996). They too are ground-feeding granivores, but they also consume human food waste and spillage (Frith *et al.* 1976). Feral Pigeons (Rock Doves) *Columba livia* were definitely released in Victoria around the middle of the nineteenth century, but may have arrived in Australia considerably earlier with the first European settlers. They are widespread in eastern, south-eastern and south-western Australia and particularly abundant in urban areas, where they nest on buildings and forage on the ground, consuming seeds, human food waste and ‘volunteer’ (deliberately given) food (Higgins and Davies 1996). Surprisingly, the ecology of these two introduced pigeons in Australia is not well documented (Higgins and Davies 1996).

The present study documented the habitat occupancy and foraging ecology of Crested Pigeons in Melbourne to elucidate factors that may have facilitated their recent colonising of the city. Simultaneously we documented the same traits for Spotted Turtle-Doves and Feral Pigeons because of their potential role as food competitors of Crested Pigeons in the city. We also recorded the extent to which all these pigeons foraged close to, and interacted with, one another, to gauge whether inter-specific interference competition operating through aggression and/or avoidance (Cresswell 1997) was frequent among them and might therefore potentially influence their urban settlement patterns.

## METHODS

### *Study area and habitats*

The study was conducted from May to August 2008 at 54 sites in six municipalities in metropolitan Melbourne (37°48'S, 144°57'E), stretching 60–70 kilometres from Melton in the north-west to Knoxfield and Cheltenham in the south-east. During the investigation, mean monthly maximum and minimum ambient temperatures in Melbourne averaged 15.5 and 8.2°C, respectively, and mean monthly rainfall was 36.9 millimetres.

Population surveys and behavioural observations were made in the five habitats defined by Crisp and Lill (2006):

- (1) Bushland (8 sites) – remnant forest or densely-planted native trees, dominated by *Eucalyptus* and *Corymbia* species,
- (2) Industrial area (10 sites) – streets dominated by commercial buildings (warehouses and factories), with few houses and little vegetation,
- (3) Open parkland (11 sites) – parks or reserves often used for recreation, dominated by open grassland, with a few shrubs and trees,

- (4) Wooded parkland (11 sites) – similar to open parkland, but with many native and/or exotic trees and shrubs, and
- (5) Streetscape (14 sites) – residential streets, lined by houses and gardens and sometimes having street trees.

These habitat categorisations were initially qualitative, so Crisp and Lill (2006) validated them by measuring 12 habitat elements at each study site. As we were using many different sites from those used by these authors, we conducted a similar, but more limited, validation exercise by recording the occurrence of these 12 and one additional element (see Table 1) in six randomly selected study sites in each habitat. We subdivided the 15 000 square metres survey transect(s) at each site lengthwise into 20 by 30 metre quadrats and recorded the presence/absence of each element in alternate (i.e. 13) quadrats. The number of study sites per habitat approximately reflected the relative occurrence of the habitat types in Melbourne. Sites were spread across 13 municipalities and among all the designated habitats present in a municipality, but within a habitat in a given municipality they were selected randomly.

### *Pigeon population density and habitat use*

Population densities (individuals per ha) of the three pigeon species were measured simultaneously on one day at each site. Surveys were conducted on two days per week throughout the study, beginning 0.5–1 hour after first light or 2–2.5 hours before dusk. The seasonal distribution of surveying was similar among municipalities and morning and afternoon survey effort was distributed similarly among municipalities and habitats. The precise order in which habitats and sites were surveyed was randomised. Belt transects (Bibby *et al.* 2000) were 30 metres wide by 500 metres long and the researcher walked along the mid-line or one edge (streetscapes and industrial areas) at a steady pace (~ 1.5 km per hr) counting all the (non-flying) pigeons in the transect. A separate count was kept of pigeons seen at each site outside the transect boundaries to provide additional information about species' presence where densities were low. Where the full width of a transect was not visible at a particular point, density estimates were adjusted appropriately. One transect was surveyed per site in industrial areas and streetscapes; in the other habitats, one to four transects were surveyed per site, depending on the site's size, so that survey effort was scaled for site area, but not directly proportionately (Platt and Lill 2006).

### *Foraging ecology*

Foraging of all three species was observed in the morning and late afternoon/early evening. Although pragmatism determined that these observations were less constrained spatially and temporally than the population surveying, we distributed them in both dimensions so as to obtain a representative, unbiased sample of foraging behaviour in the habitats that each species used significantly. Maximally five individuals per species per observation session were recorded at a site to reduce re-sampling of individuals and enhance data independence.

A focal bird's foraging was recorded by noting its behaviour during one 5-second interval in every 20 seconds, up to a maximum time of 100 seconds (i.e. up to 5 records per bird). If more than one type of foraging behaviour was observed in the interval, only the first type was recorded. This method was a compromise between

**Table 1**

(a) Abundance of 13 habitat elements in five habitats. Abundance scores are the mean number of quadrats (out of 13) per site in which an element occurred in a particular habitat. Pkld = parkland and Art. = artificial. Blank spaces indicate absence of an element in a habitat.

Habitat element	Habitats				
	Bushland	Industrial	Open Pkld	Streetscape	Wooded Pkld
<i>Eucalyptus/ Corymbia</i> spp.	12.83	5.67	5.42		8.64
Other native trees	10.22	6		8.5	7.99
Exotic trees				9.83	
Native shrubs	10.58				
Exotic shrubs				11	
Exposed soil	8.33	9.83		5.83	11.15
Grass	9.28	13	13	13	12.96
Herbs	11.78	12.33	10.17	12.83	12.21
Art. vertical structure	7.14	12.5	4.92	12	6.54
Art. sealed surface		12.83	5.75	13	
Art. unsealed surface					5.74
Buildings		7			
Houses				11.83	

(b) Percentage contribution of habitat elements to dissimilarity between pairs of habitats derived from SIMPER analysis. Blank spaces indicate zero contributions. Contributions >10% are indicated in bold. Abbreviations for habitats are B= bushland, I = industrial, O= open parkland, W= wooded parkland and S= streetscape.

Habitat element	Pair-wise habitat comparisons									
	BxI	BxO	BxS	BxW	IxO	IxS	IxW	OxS	OxW	SxW
<i>Eucalyptus/ Corymbia</i> spp.	<b>11.23</b>	<b>13.74</b>	9.35	8.51	5.95	6.18	9.6	4.48	<b>12.14</b>	7.93
Other native trees	7.87	<b>12.58</b>		7.2	7.2	8.69	8.39	7.81	<b>12.24</b>	4.91
Exotic trees			<b>10.77</b>	8.74	8.02	<b>12.55</b>	9.72	<b>11.7</b>	<b>10.94</b>	<b>10.85</b>
Native shrubs	<b>12.58</b>	<b>18.45</b>	8.88	<b>14.65</b>		3.36	4.75	4.05	8.03	
Exotic shrubs	5.19		<b>13.05</b>		7.28	<b>14.31</b>	7.3	<b>15.52</b>		<b>13.96</b>
Exposed soil	5.19	6.06	5.23	8.09	5.4	9.22	5.98	7.07	6.63	8.87
Grass	5.9	7.09	4.62	7.96						
Herbs		5.05			5.86				6.48	
Art. vertical structure	9.34	8.52	7.1	<b>10.41</b>	<b>16.67</b>		<b>12.33</b>	<b>10.3</b>		
Art. sealed surface	<b>13.78</b>	<b>10.63</b>	<b>10.9</b>	<b>12.3</b>	<b>16.05</b>		<b>14.52</b>	<b>10.74</b>	<b>13.13</b>	<b>11.1</b>
Art. unsealed surface	9.36	<b>11.05</b>	7.45	<b>12.16</b>	6.81	4.9	8.75	3.97	<b>11.58</b>	7.14
Buildings	<b>10.21</b>				<b>13.54</b>	<b>12.32</b>	<b>12.84</b>			
Houses			<b>14.22</b>			<b>21.61</b>		<b>16.9</b>		<b>17.68</b>

the 'ideal' (one record per bird to achieve complete independence of data) and the 'pragmatic' (pigeons were not encountered sufficiently often to make the 'ideal' sufficiently productive). Features noted for each foraging record were:

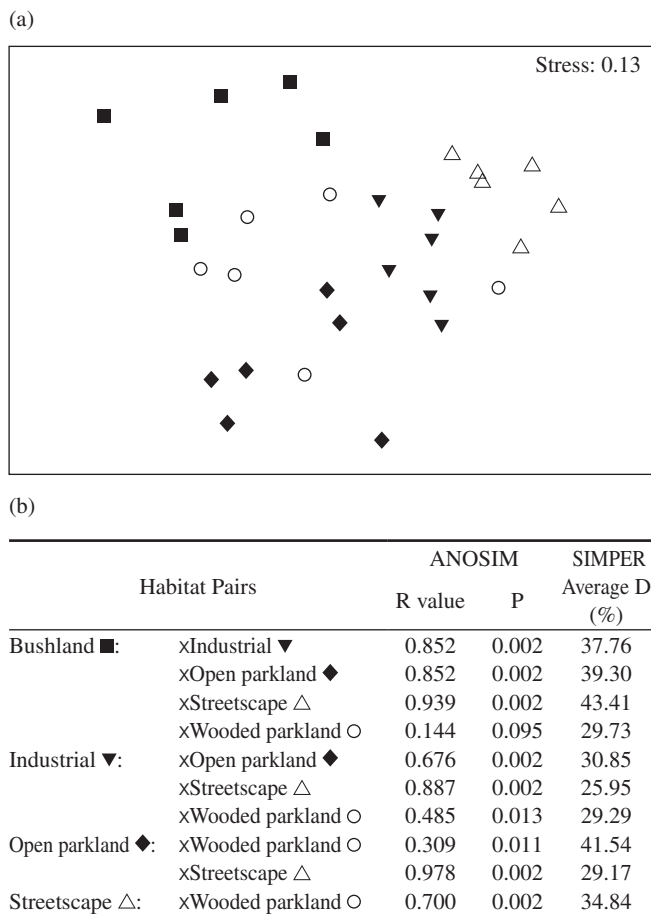
- (1) Bird's substrate – substrate on which the foraging bird was situated (categorised as grass, herb, bare ground, leaf or bark litter and artificial surface e.g. concrete, bitumen);
- (2) Food substrate – substrate on which the target food item was situated (categorised as for bird's substrate);
- (3) Food item – type of food (e.g. seed, bread), plant taxon (to species level where possible) consumed and whether item was accurately identified or not (definite or probable food item). Many items were small, fallen seeds, which were very difficult for the observer to see clearly enough to assign to a particular plant species;
- (4) Feeding behaviour pattern – gleaning (picking items off a substrate with the bill), flaking (moving bill laterally to remove loose substrate material) or 'other' (after Remsen and Robinson 1990).

#### *Foraging sociality and agonistic behaviour*

All con- and hetero-specific individuals within an estimated five metres of a focal foraging pigeon were recorded. All agonistic interactions between members of the three study species and other birds that occurred within the five-metre radius were also systematically recorded. Features noted were the species involved, form of the interaction (approach-supplant, chase or fight) and interaction outcome (no overt response, displacement of less or more than five metres and departure from the site).

#### *Data analysis*

Analyses were conducted with *Primer* v. 5.2.9 (Clarke and Warwick 2001), *Distlm* v. 5 (Anderson 2001; McArdle and Anderson 2001) and *Systat* v. 12 (SPSS Inc. 2000). Non-metric multi-dimensional scaling (nmMDS) was used to visually assess the distinctness of the five habitats based on the occurrence of the 13 measured elements. Analysis of Similarity (ANOSIM) was employed to analyse similarities in composition among sites within a habitat type and dissimilarities among habitats. The exploratory SIMPER (similarity percentage) procedure was



**Figure 1.** (a) nmMDS ordination plot of five urban habitats based on the occurrence of thirteen habitat elements. (b) dissimilarity (D) between pairs of habitat types based on ANOSIM and SIMPER analyses using the same habitat elements. Stress in nmMDS is 0.13. ■ = bushland, ○ = wooded parkland, ◆ = open parkland, △ = streetscape and ▼ = industrial area.

used to identify the habitat characteristics responsible for these similarities and dissimilarities.

Variation in the occurrence (proportion of study sites occupied) of each pigeon species among habitats was examined with generalised Fisher exact tests. Variation among study species in population densities in the suite of habitats was analysed with non-parametric multivariate analysis of variance (MANOVA). Variation in population density among habitats within species was analysed with non-parametric Kruskal Wallis one-way analyses of variance followed by *post hoc* pairwise comparisons where appropriate. Associations among four of the foraging ecology variables (bird species, habitat type, bird substrate and food substrate) were examined with loglinear modelling (Agresti 2002) using a four-way contingency table. Bushland was excluded because no study species was actually observed foraging in it and feeding behaviour patterns and food item types were also omitted because they exhibited extreme stereotypy. The most parsimonious model that fitted the data was determined by hierarchical removal of terms that did not improve the model's fit. The ratios of parameter-estimates to their standard errors,  $\lambda/(s.e.\lambda)$ , in this model indicated the

strength and direction of associations between categories within interacting pairs of variables; values more extreme than  $\pm 1.96$  were considered significant, as the probability of obtaining a value in these ranges is 0.05 (Ferguson and Takane 1989). Data are presented as mean  $\pm$  standard error (s.e.)

## RESULTS

### *Characteristics and distinctness of the urban habitats*

There was clear spatial clustering of study sites of the same habitat type in the nmMDS ordination plot based on measured habitat elements (Figure 1). Differences in the occurrence of the elements were significantly greater between than within habitats (ANOSIM Global R = 0.674, P=0.001); only the bushland  $\times$  wooded parkland comparison failed to yield a significant R value (Figure 1). Average dissimilarity between pairs of habitats was also lowest for this combination and highest for the bushland  $\times$  streetscape combination (Figure 1). Average similarity values (%) were 72.79 (wooded parkland, streetscape), 74.27 (bushland), 76.11 (open parkland) and 82.39 (industrial areas). The SIMPER procedure indicated that bushland sites were particularly distinguished by the combined presence of *Eucalyptus/Corymbia* trees (similarity 20.95%), herbs (17.74%), other native trees (14.03%), native shrubs (13.83%), exposed soil (10.77%) and grass (10.67%). Industrial areas were especially distinguished by a combination of habitat elements comprising grass (17.18%), artificial sealed surfaces (16.72%), human-made vertical structures e.g. signs and posts (15.95%), herbs (15.41%) and exposed soil (10.95%). Open parkland was characterised particularly by the combined presence of grass (29.42%) and herbs (18.91%) and streetscapes by a combination of grass (13.65%), artificial sealed surfaces (13.65%), artificial vertical structures (11.62%), houses (11.37%) and exotic shrubs (10.13%). A combination of five habitat elements, namely grass (21.74%), herbs (19.66%), exposed soil (16.27%), *Eucalyptus* and *Corymbia* (10.57%) and other native trees (10.33%) particularly distinguished wooded parkland.

### *Variation in pigeons' occurrence and population density among habitats*

The occurrence of the Crested Pigeon varied significantly among the five habitats surveyed ( $p=0.007$ , generalised Fisher exact test) (Table 2). It was absent from bushland and streetscapes, but present in 64 per cent of open parkland, 27 per cent of wooded parkland and 10 per cent of industrial sites (Table 2). The Feral Pigeon was also absent from bushland, but occurred in 27 to 36 per cent of sites in the other four habitats ( $p<0.001$ , Fisher test). The Spotted Turtle-Dove was ubiquitous and the proportion of sites in which it occurred did not vary significantly among habitats ( $p=0.581$ , Fisher test).

The pigeons' distribution among habitats was less clear-cut with respect to estimated population density. There was overall variation among the estimated population density distributions of the three species in the five habitats (pseudo  $F_{(8)} = 2.550$ ,  $P<0.01$ ) (Table 2). Crested Pigeons' population density varied significantly among habitats (KW = 12.105,  $P=0.017$ ,  $n = 54$ ), but the only significant pair-wise difference was that the density in open parkland was greater than that in bushland ( $P<0.05$ ). The Feral Pigeon's estimated population density was similar in all habitats (KW = 2.652,  $p=0.618$ ,  $n = 54$ ) despite its complete



**Table 2**

Mean ( $\pm$  s.e.) population density (per ha) and occurrence of three pigeon species in five urban habitats. Upper row is estimated population density and numbers in parentheses in lower row indicate number of sites at which species was observed inside and/or outside transects.  
 $n$  = number of survey sites.

Species	Bushland $n=8$	Industrial $n=10$	Open Parkland $n=11$	Streetscape $n=14$	Wooded Parkland $n=10$
Crested Pigeon	(0)	0.3 $\pm$ 0.3 (1)	1.6 $\pm$ 1.3 (7)	(0)	0.1 $\pm$ 0.1 (3)
Feral Pigeon	(0)	13.9 $\pm$ 10.6 (3)	1.7 $\pm$ 1.4 (3)	2.5 $\pm$ 1.5 (5)	2.2 $\pm$ 1.6 (3)
Spotted Turtle-Dove	0.7 $\pm$ 0.7 (3)	0.2 $\pm$ 0.2 (7)	0.1 $\pm$ 0.1 (7)	2.6 $\pm$ 0.8 (10)	0.8 $\pm$ 0.4 (7)

absence from one, whilst the Spotted Turtle-Dove's density varied significantly among habitats (KW = 14.075,  $P=0.007$   $n = 54$ ), although this was not reflected in any significant *post hoc* pair-wise differences between habitats ( $P>0.05$ ). The limited variation in population density between habitats in pair-wise comparisons for all species probably reflected their highly gregarious behaviour, which meant that they were often either present at a site in large numbers or completely absent. Thus Spotted Turtle-Doves occurred at densities of 2–9 birds per hectare in nine of the streetscape sites, but were absent from the other five sites, and Feral Pigeons occurred at densities of 36 and 103 birds per hectare at two industrial sites, but were absent from the other eight such sites.

#### Diet and foraging behaviour

As with urban Common Mynas *Acridotheres tristis* (Crisp and Lill 2006), it was difficult to identify with great accuracy many of the food items consumed, because they were very small and situated on or close to, the ground. However, seeds were definitely very common in the diet of all pigeon species. Most definite and probable food items taken from living plants were the seeds of three grass (family Poaceae) and five herb (families Chenopodiaceae, Aizoaceae and Geraniaceae) species, only two of which are Australian natives. Most of the herbs are regarded as weeds (Richardson *et al.* 2007). Crested Pigeons probably fed on seeds still attached to the raceme of three grasses and three herbs, namely *Poa annua* (which occurred at 62% of their foraging sites), *Pennisetum clandestinum* (15% of sites) and *Cynodon dactylon*, *Chenopodium album*, *Galenia pubescens* and a *Geranium* species (all at 8% of sites). Feral Pigeons definitely consumed attached seeds of one grass and two herb species, namely *P. annua*, *G. pubescens* and an *Erodium* species (all occurring at 13% of their foraging sites). Spotted Turtle-Doves probably fed on attached seeds of two grass and three herb species, which were *P. annua* (present at 44% of their foraging sites), *P. clandestinum* (22%), *G. pubescens*, a *Geranium* species and an *Arctotheca* species (all at 11% of sites).

Feeding behaviour was extremely stereotyped among the pigeon species, all but five of the 436 records obtained from 101 individuals comprising gleaning. Four Feral Pigeons were observed flaking and one picked up and manipulated bread with its bill. Unidentified seeds featured prominently in all species' diets and occurred at 25–38.5 per cent of the foraging sites used by the various pigeon species.

**Table 3**

$\lambda$  / (s.e. $\lambda$ ) values for the four significant interaction terms in the most parsimonious loglinear model of foraging. Significant associations between factors are shown in bold type. Positive (unsigned) and negative (-) values indicate the direction of the associations. CP = Crested Pigeon, FP= Feral Pigeon, STD = Spotted Turtle-Dove, Ind = industrial, OPk = open parkland, Str = streetscape, WPk = wooded parkland and Art. = artificial.

Habitat x	Bird species		
	CP	FP	STD
Industrial	-0.617	0.872	-0.234
Open parkland	<b>6.805</b>	-1.334	<b>-5.062</b>
Streetscapes	-1.81	-1.075	<b>3.29</b>
Wooded parkland	<b>-2.266</b>	1.324	1.088

Bird substrate x	Habitat			
	Ind	OPk	Str	WPk
Art. surface	1.012	<b>-2.655</b>	<b>3.713</b>	-1.5
Bare ground	-0.937	1.805	-1.912	<b>2.19</b>
Grass	-1.903	<b>5.667</b>	<b>-1.974</b>	0.43
Herb	1.312	-1.938	1.13	-0.556
Litter	0.749	-0.594	-0.372	0.103

Food substrate x	Habitat			
	Ind	OPk	Str	WPk
Art. surface	1.53	<b>-2.241</b>	1.449	-0.641
Bare ground	-0.447	<b>3.572</b>	-0.761	-1.442
Grass	<b>-2.426</b>	1.632	-1.354	<b>4.203</b>
Herb	0.76	-1.049	1.459	-1.187
Litter	0.889	-0.506	-0.558	0.084

Food substrate x	Bird substrate				
	Art. surface	Bare ground	Grass	Herb	Litter
Art. surface	<b>4.155</b>	-1.376	<b>-2.15</b>	0.173	0.206
Bare ground	-1.195	<b>6.466</b>	-1.552	0.601	-1.217
Grass	<b>-2.251</b>	0.662	<b>10.49</b>	<b>2.088</b>	<b>-2.372</b>
Herb	0.28	-1.767	-0.233	1.891	0.002
Litter	-0.216	-1.41	<b>-2.467</b>	0.851	<b>4.009</b>

The most parsimonious loglinear model of foraging contained four first order terms (bird species, habitat type and bird and food substrates) and four second order interaction terms (bird species  $\times$  habitat, bird substrate  $\times$  habitat, food substrate  $\times$  habitat and food substrate  $\times$  bird substrate). The only significant difference among the pigeon species was in the use of habitat for foraging. Crested Pigeons foraged more than expected in open parkland

**Table 4**

Percentage of foraging observations in which various other birds or no birds were within 5 m of the focal pigeon.  $n$  = number of records.

Focal species	$n$	Species within 5 metres				
		Crested Pigeon	Feral Pigeon	Spotted Turtle-Dove	Other spp.	None
Crested Pigeon	210	100	0	2	12	0
Feral Pigeon	111	14	100	0	34	0
Spotted Turtle-Dove	116	13	1	84	17	16

and less than expected in wooded parkland and Spotted Turtle-Doves more than expected in streetscapes and less than expected in open parkland (Table 3).  $\lambda$  / (s.e. $\lambda$ ) values indicated that the two pigeon species that fed in streetscapes particularly used artificial ground surfaces for foraging. Collectively, the three pigeon species particularly used grass in open parkland and bare ground in wooded parkland as their foraging substrate, but interestingly, however, food was particularly obtained from bare ground in the former and from grass in latter habitat. Despite this discrepancy, there was significant correspondence overall between use of substrates for foraging and the substrates from which food was obtained (food substrate  $\times$  bird substrate; Table 3).

#### Foraging sociality and agonistic interactions

Crested and Feral Pigeons always foraged within five metres of con-specifics and Spotted Turtle-Doves did so on 84 per cent of occasions (Table 4). Members of each pigeon species foraged close to members of at least one of the other two species, but not very frequently ( $\leq 14\%$  of records for any species). Members of all pigeon species also foraged close to members of non-pigeon species, Feral Pigeons in particular doing so on 34 per cent of occasions. Crested Pigeons foraged within five metres of exotic Common Starlings *Sturnus vulgaris* and House Sparrows *Passer domesticus*. Pacific Black Ducks *Anas superciliosus*, Silver Gulls *Larus novaehollandiae*, exotic Common Mynas and Dusky Moorhens *Gallinula tenebrosa* foraged close to either Feral Pigeons or Spotted Turtle-Doves.

Although all or much of the pigeons' foraging was conducted close to con- or hetero-specifics, only three agonistic interactions involving members of any of the pigeon species were observed during the 3.5-month investigation (i.e.  $\sim 0.13$  interactions per 2–3 hr session observing foraging). One involved a chase between two Crested Pigeons and the others a Noisy Miner chasing a Feral Pigeon. All interactions displaced the target bird, but only one of them for more than five metres.

## DISCUSSION

#### Habitat use and population density

The analysis of habitat characteristics showed that the habitats were fairly distinct. Successful avian colonisers of cities are rarely ubiquitous or evenly distributed across the urban habitat matrix (White *et al.* 2005; Garden *et al.* 2006). This was partly the case in the present investigation, in which habitat use also varied among the study species. Crested and Feral Pigeons were absent from bushland and the former species also from streetscapes, but Spotted Turtle-Doves occurred in all five habitats. In terms of occurrence, the Crested Pigeon was most strongly associated with open parkland and in terms of population density the Spotted Turtle-Dove appeared most abundant in streetscapes, although this was not reflected in the pair-wise *post hoc* comparisons. However, the observations of

habitat use for foraging strongly supported these associations inferred from the population surveys (Table 1). Our findings broadly concur with published accounts particularly linking the occurrence (or relative occurrence) and foraging of urban Crested Pigeons in New South Wales and Brisbane with suburban open parkland and of urban Spotted Turtle-Doves in Melbourne and Brisbane with suburban streetscapes (Higgins and Davies 1996; Green 2003; White *et al.* 2005).

The Crested Pigeon may, in a sense, be particularly suited to urban open parkland because its natural habitat is lightly wooded grassland. However, streetscapes also often contained the grasses and herbs which provided the seeds that dominated this species' urban diet (Table 2), yet it did not occur in them. Open parkland appeared to have a greater abundance of these food resources, but this could not be ascertained accurately from the presence/absence method of sampling habitat characteristics that we used. Crested Pigeons and Spotted Turtle-Doves both also exploit human food waste and spillage (Frith *et al.* 1974, 1976), but Turtle-doves probably do this more than Crested Pigeons in Melbourne, which might partly explain their strong propensity to forage in streetscapes, where such resources are relatively abundant because of the substantial human traffic. Although predation pressure on birds is thought to be lower in cities than in more natural habitats (Faeth *et al.* 2005), the difference in habitat usage of these two species could possibly also reflect differing vulnerabilities to predation and/or to different suites of predators. Ground-foraging birds are likely to be more visible to predators in open parkland than in streetscapes in Melbourne because cover is fairly sparse in the former, whilst residential streets often have adjacent gardens with dense vegetation. Beyond the present study, Crested Pigeons have occasionally been observed in Melbourne streets perching on telephone wires and television aerials, but not foraging, (AL, pers. obs.); conceivably on a citywide basis they do sometimes forage in streets, which have some grassy substrate on their sidewalks.

The Feral Pigeon's similar level of occurrence and population density in all habitats except bushland did not entirely accord with qualitative statements (Higgins and Davies 1996) that this strongly commensal species (del Hoyo *et al.* 2004) is particularly abundant in urban streets, where human food waste is common. There are four likely and not mutually exclusive hypotheses to explain this discrepancy: (1) in the northern hemisphere, Feral Pigeons' occurrence in cities is positively correlated with human population density and increases centripetally (Jokimaki and Suhonen 1998; Sacchi *et al.* 2002), but inner city streets provided only a subset of our streetscape records, (2) the disparity could reflect the fact that the streetscapes that we surveyed were mainly residential rather than commercial (e.g. shopping strips), (3) the discrepancy could have occurred partly because our investigation occurred in the non-breeding season, when proximity to buildings providing nesting sites may be less important in determining Feral Pigeons' urban

distribution (Sacchi *et al.* 2002) and (4) the substantial within-habitat variation in population density of Feral Pigeons indicated that even more extensive population surveying is desirable for this highly gregarious and mobile species. Green (2003) found that Feral Pigeons dominated pigeon assemblages in inner city streets and parks in Brisbane, giving some support to the first of these hypotheses.

#### *Diet and foraging behaviour*

All study species consumed some seeds of grasses and herbaceous weeds that were still attached to the racemes of living plants, but they also ate many more detached seeds, which were impossible to identify with precision by observation. Nonetheless, the general picture that emerged of the pigeons' diets as comprising mostly grass and herb seeds agreed quite well with accounts based on gut content analysis. Crested Pigeons' diet in rural New South Wales comprised 85.5 per cent seeds of exotic weeds and crop plants, 13.5 per cent leaves and less than 1 per cent animal material (Frith *et al.* 1974). In our study, grass seeds (particularly of *P. annua*) appeared to be even more prominent in the diet. Feral Pigeons elsewhere in Australia and in Europe, Canada and South Africa consume grass and weed seeds, human food waste and 'volunteer' and livestock food (Frith 1982; Lefebvre and Giraldeau 1984; Little 1994; Higgins and Davies 1996; Sol *et al.* 1998; del Hoyo *et al.* 2004; Rose *et al.* 2006). We found a lesser reliance on human food waste and volunteer food, but this probably resulted from obtaining fewer records from inner city and commercial streets, where this behaviour is prominent (AL, pers. obs.), than in these other studies. The diet of the Spotted Turtle-Dove is not well documented, but Frith *et al.* (1976) showed that in Perth, Sydney and Melbourne it too consumed exotic grass and herb seeds, human food waste and spillage and livestock food. Human food waste and livestock food featured less in its diet in our investigation, probably because we did not sample near stables, in shopping malls etc. Published accounts and our findings together indicate that in Australian cities the diets of Feral Pigeons and Spotted Turtle-Doves overlap that of Crested Pigeons substantially.

Feeding behaviour was extremely stereotyped among the three pigeon species. Almost all food acquisition involved gleaning, although manipulating human food waste and volunteer food is probably more common in Feral Pigeons and Spotted Turtle-Doves in some urban locations with heavier human traffic than those which we studied. All three species exhibited similar patterns of foraging substrate use, which for the species collectively varied significantly among habitats in what appeared to be a density-dependent manner. Thus artificial surfaces, herbaceous weeds and leaf/bark litter predominated as foraging substrates in industrial areas, bare ground and grass in open parkland, artificial surfaces and herbs in streetscapes and grass in wooded parkland.

#### *Foraging sociality and agonistic behaviour*

All three pigeon species always or mostly foraged gregariously with con-specifics, but aggressive interactions were extremely rare and had a negligible effect on foraging behaviour. Thus intra-specific contest competition, a common cost of social foraging (Caraco *et al.* 1980) that might be expected to occur frequently in cities where avian population densities tend to be relatively high (Faeth *et al.* 2005), was virtually absent in the

habitats studied. This social, non-aggressive foraging syndrome may occur in granivorous birds in the non-breeding season partly because seeds are often patchily distributed but locally superabundant, which means that they are more efficiently found by groups, but there is little need for competition once a patch is found (Krebs and Davies 1987). Foraging with the other pigeon species when they co-occurred at a site was relatively infrequent and did not involve inter-specific contest competition. This did not exclude the possibility that other types of exploitative interference competition promoted the partial spatial segregation of foraging at the site and, to lesser extent, habitat level observed among the pigeon species. More efficient predator detection and avoidance are also benefits of avian flocking, particularly in habitats with limited cover (Kenward 1978; Lima 1995), and may have been influential in the study species. A reduction in individual, but an increase in group vigilance as a function of flock size has been demonstrated for Spotted Turtle-Doves in Melbourne (Sadedin and Elgar 1998).

#### *Possible factors facilitating urban colonisation by Crested Pigeons*

The Crested Pigeon's evolutionary history in open woodland, savanna and scrubland (Higgins and Davies 1996) probably 'pre-adapted' it to colonise both rural pastoral land and urban open parkland. Both habitats contain abundant grasses and herbs that provide seed resources similar to those likely to have dominated the pigeon's diet in its original natural habitat, except that they are exotic. Some of the grasses exploited in urban open parkland even seed prolifically despite being mowed regularly (Huff 2002). A natural tendency to feed gregariously should also afford Crested Pigeons some protection from predation in open parkland, which has limited cover. Thus phenotypic (behavioural) plasticity was probably not a major prerequisite for successful urban foraging in this species (Møller 2008).

Although the other two co-habiting pigeons apparently had a very similar diet and definitely had extremely similar foraging behaviour to that of Crested Pigeons in Melbourne, there was some limited segregation among the three species by habitat occupancy. Moreover, where they co-existed they fed close together fairly infrequently. The types of seeds that comprised much or all of the three species' diets appear to be very abundant in Melbourne in autumn and winter. Although we did not measure seed abundance, Lowry and Lill (2007) showed that in Melbourne's open parklands, grass and herb seeds generally, and those of the grasses *P. annua* and *P. clandestinum* in particular, were abundant in winter. Thus even though these seeds are also consumed by Red-rumped Parrots *Psephotus haematonotus* and possibly some other bird species in some open parklands (Lowry and Lill 2007), they are currently probably not a limiting resource for the pigeons. The absence of inter-specific aggression during foraging suggested that contest competition for food (Lefebvre and Giraldeau 1984) was negligible among the study species in autumn/winter. Establishing many parks and reserves in Melbourne appears to have facilitated urban colonisation by Crested Pigeons and other native and exotic granivorous birds (Lowry and Lill 2007).

#### *Future studies*

Our 'snapshot' study, a first attempt at identifying factors facilitating residence of Crested Pigeons in Melbourne, needs



to be expanded to cover: (a) spring and summer, when breeding occurs and energy demands are probably different (b) more years, in order to account for inter-annual weather variations (especially in rainfall) that could affect food resource abundance, and (c) other Australian conurbations recently colonised by Crested Pigeons to determine whether the present results have broader applicability. Further, although foraging behaviour was remarkably similar in the three pigeons studied, their diets need to be quantified more precisely, preferably through non-invasive techniques, although this would be challenging. Although we conducted 54 surveys, the considerable within-habitat variation in population density yielded some anomalous results, so even more extensive surveying is needed in future studies. More broadly, to fully understand the factors facilitating urban colonisation by Crested Pigeons, we need to examine additional aspects of their urban ecology. For example, urban Crested Pigeons and Spotted Turtle-Doves might compete for nest sites, because both commonly nest in the dense foliage of low trees and shrubs, whereas urban Feral Pigeons mostly nest in and on buildings (Higgins and Davies, 1996). An additional incentive to study Crested Pigeons and other native colonisers of Melbourne is that the city is much younger than most of the European cities in which urban colonisers have been investigated. Are the factors that influence colonisation similar in both hemispheres?

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