Behavioural and Ecological Keys to Urban Colonization by Little Ravens (*Corvus mellori*)

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Abstract: Avian urban colonization is thought to be facilitated by a capacity for innovative feeding, ecological generalism and social foraging. However, the relative importance in exploiting urban resources and avoiding urban predators of being inherently 'pre-adapted' to the urban environment or adjusting to it through phenotypic plasticity requires more examination. These issues were explored in a native 'urban adapter', the Little raven *Corvus mellori*, by comparing its foraging ecology, group size and nest site use in Melbourne, Australia, and the surrounding exurban environment. Urban individuals manipulated human food waste and gleaned from sealed surfaces more than exurban conspecifics (suggesting behavioural flexibility), but foraging behaviour and substrate use were broadly similar in both environments (suggesting 'preadaptation'). Little ravens foraged close to conspecifics and heterospecifics more frequently in the urban than the exurban environment, but some potential dietary competitors rarely foraged near urban Little ravens, possibly indicating some niche partitioning. Mean urban rate of agonistic interaction with other bird species was low (0.023 interactions per foraging raven observed). Although displacement of a raven >10 m occurred in 61-70% of such interactions, the displaced individual usually rapidly resumed foraging nearby. Thus aggressive, interspecific interference competition for food appeared limited. Large groups of Little ravens were twice as common in the exurban as the urban environment, which was inconsistent with the hypothesis that social foraging facilitated urban colonization. Nest tree type (predominantly eucalypts), size and isolation were similar in urban and exurban environments, but urban nests were significantly more concealed. We suggest that 'preadaptation', behavioural innovation and a relative lack of significant, interspecific food competition have contributed to urban colonization by Little ravens.

Keywords: Foraging competition, group size, innovative feeding, nest site characteristics, 'pre-adaptation', urban colonization.

INTRODUCTION

Increasing urbanization globally has stimulated both a greater awareness of the need to conserve urban biodiversity and a proliferation of the kind of research that is required as a foundation for that conservation effort [1, 2]. Urbanization drastically alters the natural environment; some species thrive under the altered circumstances ('urban exploiters' and 'adapters'), whilst others ('urban avoiders') cannot adjust to the altered environment [3].

It is often suggested for bird species that successfully colonize cities that one facilitating factor is that food abundance is greater than that in their exurban environment (EXU$_{env}$) [4-6]. Proposed reasons for this greater abundance include: (a) availability of additional, novel foods, such as human food waste and food supplements intentionally provided at feeding stations [7, 8], (b) extension of flowering and fruiting seasons, resulting from the urban heat sink effect and artificial watering regimes [9, 10], and (c) planting of multiple, non-indigenous plant species that increase the amount and seasonal availability of nectar, pollen and fruit [11, 12]. A second facilitating factor may be a low level of interspecific food competition, probably resulting partly

from the reduced species richness in urban bird communities, which may also effectively increase food availability for urban adapters [13, 14]. However, the combined effect of increased food abundance and low interspecific food competition must be substantial in order to counteract the effect of an increased population density and intraspecific competition level in the urban adapter [15-17].

Another facilitating factor may be social foraging, given the proven benefits of flocking in detecting predators, locating food and particularly learning about novel food sources [18]. In contrast, nest sites may be fewer in cities for many bird species because of the reduction and fragmentation of natural vegetation [19], although hole-nesters that can exploit the many cavities in city buildings may be an exception [14].

There are two hypothesised reasons for corvids' well-known ability to colonize cities [20]. Firstly, they have a great capacity for learning innovative feeding behaviours [21, 22], such as exploiting human food waste, which is presumably facilitated by their particularly large brain [20]. Secondly, they are ecological generalists, so the altered conditions encountered in cities are more likely to fall within the broader range of environmental tolerance exhibited by such species [23, 24]. These two traits frame, with respect to resource use, one of the intriguing issues about corvids' ability to colonize cities, namely the relative importance of being:

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(a) sufficiently phenotypically plastic to adjust rapidly behaviourally to the altered resource base [8, 25], and (b) inherently suited to exploit that base [18, 26]. However, 'preadaptation' can only facilitate urban colonization if an unoccupied niche exists for the colonizer or it can 'outcompete' the current occupant(s) of a suitable niche [18].

Little ravens (*Corvus mellori*) (LRs), endemic to southeast Australia [27], mainly inhabit grassland and dry, open, sclerophyll woodland in the EXU_{env}, but are also common in urban parks, gardens and road corridors. They have colonized metropolitan Melbourne and Adelaide and some regional Victorian and South Australian towns and cities. They are omnivorous, consuming insects, small vertebrates, carrion and fruit [28], and are known predators on other birds' eggs and nestlings [29]. Little ravens mainly feed on the ground, reputedly often in flocks in the non-breeding season, and their large, stick nests are either solitary or loosely clumped [27]. The one major published study of the species' ecology was conducted predominantly on agricultural land in New South Wales [28, 30].

The present study compared foraging behaviour and food competition, group size and nest and nest-site characteristics of urban and exurban LRs. The aim was to elucidate the extent to which LRs' urban colonization success hinges on: (a) being inherently suited to exploit urban food resources and nest-sites, and avoid urban predators, (b) being able to adjust behaviourally to exploit novel food sources, and (c) a lack of effective interspecific competition for these resources.

METHODS

Study Area

Foraging ecology, aspects of sociality and nest and nest-site characteristics of free-living LRs were documented from July, 2012 to January, 2014 in urban (U_{env}) and EXU_{env} environments in southern Victoria, Australia. The EXU_{env} sampled extended 91 km east, 140 km north and 60 km west of Melbourne (37.7833°S, 144.9667°E). It mainly comprised agricultural land used for grazing stock, growing grass to make hay and growing various crop plants, occasionally interspersed with patches of open woodland. The U_{env} was primarily urban Melbourne, with a few observations from regional Victorian towns and cities. Most observations were made in, and adjacent to, roadscapes (road plus adjoining vegetation corridor), in farmland and in open parkland/woodland. Although LRs also inhabit dry sclerophyll eucalypt forest [27], we sampled this habitat minimally. Little ravens were distinguished from co-occurring Australian ravens (*C. coronoides*) mainly by their distinctive vocal behaviour; it is known that the ravens in urban Melbourne are mainly *C. mellori* [31].

Observation Regime

All field observations were made by the same observer. Observations of foraging and associated agonistic behaviour were made from July, 2012-July, 2013 during 139 observation sessions, each of which lasted 4-5 hours. Observations were made from a vehicle with tinted windows (and occasionally on foot) at all times of day from ~ 1 hr after first light until 1 hr before dusk. Using the vehicle as a hide

meant that we could typically get within 5-20 m of focal foraging birds in streetscapes, but ravens foraging in paddocks and parks could be up to 40 m away, necessitating the use of high-powered binoculars. The size of all Little raven groups encountered (and any associated agonistic behaviour) was recorded on 331 days spread evenly over the same one-year period.

Measurement of Foraging Behaviour and Competition

Foraging records were obtained from a large number of sites spread throughout the U_{env} and EXU_{env}. A locality chosen for study on a given day was searched systematically and all LRs encountered were observed, so that foraging data for the two environments should be representative and unbiased. It is unlikely that we re-sampled particular individuals on the same day, because typically we had to drive a considerable distance between sightings and we never back-tracked within an observation session. Food items were identified where possible, but most could not be seen clearly enough.

Foraging behaviour was categorised as:

1) Gleaning – picking (or prising) food items off a surface with the beak, occasionally after a short pursuit or a vertical leap. For analytical purposes, this category also included tearing pieces off carcasses, which occurred relatively infrequently.

2) Probing – obtaining food items from beneath a substrate by piercing the surface with an open beak once or 'hammering' multiple times.

3) Sweeping – pushing or pulling substrate (e.g. hay or litter) aside with the beak and accessing the food items underneath.

4) Manipulating – accessing human food waste in a container (or occasionally other food items not in a container) using the beak and often a foot to anchor the item.

The main substrates occupied by a focal foraging raven and the substrate from which it obtained the food item were categorised as: (1) sealed ground surface (bitumen or concrete); (2) gravel; (3) soil and sand; (4) grass; (5) leaf and bark litter; (6) roofs of buildings, which were usually composed of tiles or metal; (7) garbage receptacle; (8) infrastructure (telephone poles and wires, street lamps and fences), and (9) trees.

For each foraging record, we also noted:

(a) The number of LRs or other birds that were within a visualised 10 m of the focal bird.

(b) Whether there was any inter- or intraspecific aggression involving the focal individual, and its nature and outcome.

The type of site in which the record was obtained was classified as: (1) roadscape (including car parks), (2) open parkland/woodland, (3) garden, (4) paddock, (5) forest, (6) beach, (7) golf course, or (8) school grounds. However, this variable was not included in statistical comparisons of the two environments, because the range of site types available and which could be monitored was much more restricted in the EXU_{env}.

Measurement of Group Size

Group size was recorded accurately for up to 19 individuals, but larger groups were recorded as containing ≥20 ravens because accuracy became difficult. Sizes were recorded at all times of day, except that we did not make counts at communal roosts and only a few on LRs approaching or leaving such roosts. Any intraspecific or interspecific agonistic behaviour involving group members and its nature and outcome were systematically documented. Type of site in which the group was observed was also recorded in exactly the same manner as for foraging records. Although the U_{env} sample was 1.8 times larger than the EXU_{env} sample, the latter was large enough to be representative.

Measurement of Nest and Nest Site Characteristics

Nest sites spread throughout the U_{env} and EXU_{env} were mostly found by observing breeding birds' movements, but also by examining likely places. Nest tree characteristics recorded were:

1) Type (eucalypt, Cupressaceae species – cypresses and cypress-pines, and other);

2) Morphometrics -height, canopy depth and trunk diameter at breast height (dbh)

3) Isolation index - number of trees of similar height within 30 m of nest tree

4) Concealment - a categorical nest concealment descriptor which was a visual estimate always by the same observer of extent to which nest was visible from below and 30 m laterally at ground level. It was scored as: (a) very visible, (b) moderately visible and (c) largely hidden.

Habitat in which the nest tree occurred was recorded, but not included in significance testing for the same reasons as those for foraging behaviour.

Distances (± 1 m) were measured with a laser range finder (Bushnell Yardage Pro Sport 450™), heights (± 0.1 m) with a Haglöf electronic clinometer™ and trunk dbh (±1 cm) with a tape measure.

Data Analysis

Inferential statistical analysis was conducted with *Systat* v.13.1 (Systat Software Inc., Chicago). Data transformation was conducted where appropriate.

To increase independence of, and reduce pseudoreplication in, the foraging data:

(a) We only recorded a second or third foraging record for a focal raven if it changed some aspect of its foraging (i.e. type of site, substrate or behaviour) between records.

(b) When LRs were in large flocks, only one or two records per flock-member were obtained.

(c) Sites from which foraging data were collected were only sampled once.

For both foraging behaviour and foraging substrate use, *post hoc* analysis of (1) first records for individuals (i.e. the first of possibly up to three records obtained from a focal bird), (2) total records for individuals and (3) total records

minus those for all but three individuals in flocks of ≥ 20 ravens, gave the same outcome, so only data summaries and test outcomes for total records are presented. *Post hoc* examination also revealed that substrates used by foraging LRs and those from which the food items were actually obtained were strongly correlated (Pearson $r_{(2,279)} = 0.941$), so only the former was considered in analysis. The data for foraging behaviour and substrates were frequencies, so chi squared analyses of independence and Fisher exact probability tests were used to examine differences between the U_{env} and EXU_{env}.

Nest tree and nest characteristics were compared between the two environments with independent *t* tests and χ^2 tests of independence. Although group size records were obtained from a large number of sites in both environments, some birds were probably sampled multiple times. Consequently group size data were not considered entirely independent, not subjected to significance testing and are interpreted conservatively.

RESULTS

Diet and Foraging Behaviour

First foraging records for individuals were obtained from eight types of urban site, but principally roadscapes and open parkland. Records for the EXU_{env} came from just three site types, with paddocks and roadscapes predominating.

Gleaning comprised 53% and probing 39% of the 3,691 foraging behaviour records obtained for both environments. The profiles of all foraging behaviours used by focal birds differed in the two environments ($\chi^2_{(3)} = 128.71$, P<0.001). The standardized χ^2 residuals (Fig. **1** legend) were all > 2 and indicated that this disparity resulted mainly from urban ravens performing proportionally more gleaning and manipulation, and less probing, than exurban ravens (Fig. **1**).

The predominant substrates of the 10 used for foraging in the two environments (n= 2,804 records) were grass (63.2% of records), sealed ground surfaces (13.1%) and soil/sand (12.4%). The profiles of substrates used for foraging derived from all records obtained differed between the U_{env} and EXU_{env} ($\chi^2_{(9)}$ =577.559, P<0.001) (Fig. **2**). All standardized χ^2 residuals, except those for gravel and leaf litter substrates, were substantially > 2 (Fig. **2** legend). They indicated that the largest environment differences were that urban LRs foraged on sealed surfaces, buildings and infrastructure more, and soil and sand less, than exurban ravens.

Identified food items consumed during first feeding records of focal birds and the number of LRs observed consuming them were: human food waste (including potato chips, bread, meat, pies) (U_{env} 110, EXU_{env} 17); stock food (EXU_{env} 12); silky oak nectar (U_{env} 6); mammalian carrion (kangaroo, possum, house mouse) (U_{env} 3, EXU_{env} 1); avian carrion (Common blackbird, Sulphur-crested cockatoo) (U_{env} 3, EXU_{env} 1); unidentified natural vegetation component (U_{env} 1, EXU_{env} 3); insects/invertebrates (including caterpillar and spider) (U_{env} 3); *Eucalyptus* seeds (U_{env} 2); unidentified vertebrate carrion (U_{env} 1, EXU_{env} 1); fruit (U_{env} 1). It is highly likely, given the behaviour and substrates involved, that most other food items consumed during first feeding records were invertebrates or detached plant parts.
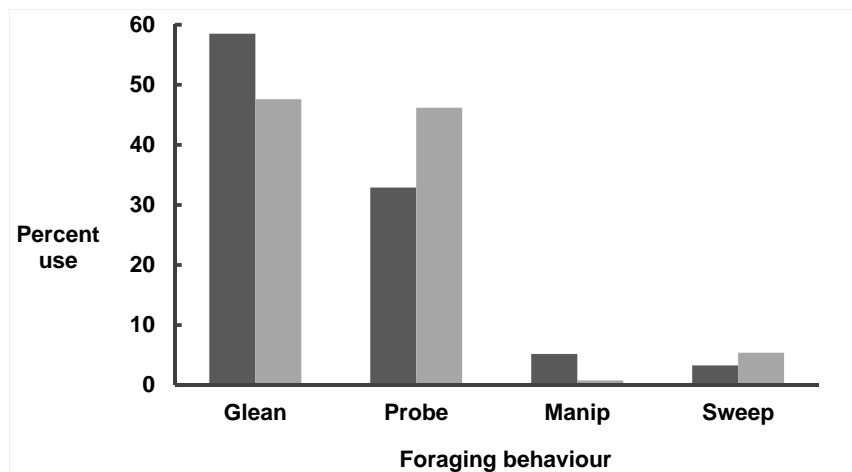
Fig. (1). Percentage use of foraging behaviours by Little ravens in urban and exurban environments. Darker columns= urban environment, lighter columns = exurban environment. Manip = manipulation. Standardized residuals from χ^2 contingency test based on all records (U_{env} given first, EXU_{env} second) were: *Glean*, +3.18 and -3.26; *Probe*, -4.48 and +4.59; *Manipulate*, +5.31 and -5.44; *Sweep*, -2.10 and +2.15.
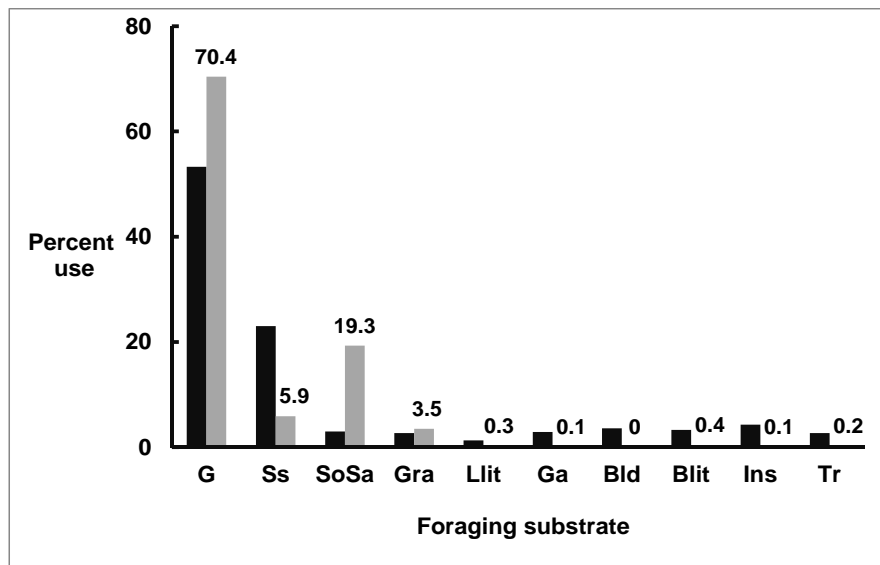
Fig. (2). Percentage use of foraging substrates by Little ravens in urban and exurban environments. Substrate key: G= grass, Ss= sealed ground surface, SoSa = soil and sand, Gra = gravel, Llit= leaf litter, Ga = garbage receptacle, Bld= building, Blit= bark litter, Ins= infrastructure and Tr = tree. Percentages shown numerically for exurban environment for clarity because some values were very small. Standardized residuals from χ^2 contingency test based on all records (U_{env} given first, EXU_{env} second) were: G, -4.272 and + 3.656; Ss, + 9.368 and -8.036; SoSa, -9.155 and + 7.849; Gra -0.822 and + 0.700; Llit, + 2.475 and – 2.110; Ga, + 4.906 and -4.249; Bld, + 5.892 and -5.0; Blit, + 4.249 and -3.849; Ins, + 6.183 and – 5.295; Tr, + 4.389 and – 3.801.

Additionally, in second or third feeding records for focal birds, LRs consumed apple cores, watermelon rind, attached pine seeds, ornamental plums and a cigarette butt. Food caching was observed in just 0.05% of the nearly 3,700 foraging observations made.

Sociality During Foraging

Overall, Little ravens spent their foraging time as follows:

(1) Solitarily, 17%

(2) Close to conspecifics only, 75%

(3) Close to conspecifics and other bird species, 7%

(4) Close to heterospecific bird species only, 1%.

When the influence of very large raven flocks was partitioned out, this association profile differed between the U_{env} and EXU_{env} ($\chi^2_{(3)}$ = 16.510, P<0.001, n=686) (Table **1**) in that simultaneously foraging close to conspecifics and other bird species was relatively more common in the U_{env} than the EXU_{env}. Three native (Noisy miner, Magpie-lark, Australian magpie) and two exotic (Common myna and Common starling) bird species foraged close to LRs in both environments. Exotic Rock doves only foraged near LRs in the U_{env}, but on just 0.5% of occasions, whilst native Galahs, Sulphur-crested cockatoos (each 2.5% of occasions), Straw-necked ibis (1%) and Grey butcherbirds (0.1%) only foraged near LRs in the EXU_{env}, but again on just a small percentage of occasions. Common mynas foraged near LRs more than any other species did in the U_{env} (3.3% of occasions), but Australian magpies held this position in the EXU_{env} (4.3% of occasions).

Table 1.   Percentage of occasions on which focal foraging Little ravens were or were not within 10 m of other birds.

Environment	Solitary	With LR only	With LR and other species	With other species only	Sample size
Urban	22.4	68.3	8.1	1.2	630
Exurban	15	77.9	6.8	0.3	1264

LR = Little raven

Aggressive Behaviour

Interspecific Interactions

The frequency of interspecific, aggressive interactions was low in both environments. An encounter occurred during just 2.3% and 1.5% of first foraging observations of focal LRs in the U_{env} and EXU_{env}, respectively ($\chi^2_{(1)}$ = 0.990, P= 0.320). Little ravens interacted agonistically with 10 other bird species in the U_{env} and 6 in the EXU_{env}, with Australian magpies and Magpie-larks being involved in both environments. However, LRs only had more than 5 agonistic encounters in total with three species, two of which they interacted with only in the U_{env} (Table **2**).

Table 2.   Little ravens' involvement in interspecific agonistic interactions.

		Combatant species	
Encounter variables	Noisy miner	Common myna	Australian magpie
Number of encounters	**18** 0	**15** 0	**23** 35
Percent initiated by LR	**0**	**46.2**	**8.7** 2.9
Percent encounter types:			
Approach	**5.6**	**6.7**	**0.0** 0.0
Threaten	**5.6**	**6.7**	**5.0** 8.3
Attack	**33.3**	**13.3**	**30.0** 75.0
Pursuit	**55.6**	**73.3**	**65.0** 16.7
Percent encounter outcomes:			
LR retreat > 10m	**61.1**	**40.0**	**70.0** 22.9
LR retreat < 10m	**11.1**	**13.3**	**10.0** 31.4
No retreat by LR	**22.2**	**13.3**	**10.0** 45.7
Other	**5.6**	**33.3**	**10.0** 0.0

Data are for the three species with which LRs had > 5 interactions. Bold font numbers are for urban environment and non-bold for exurban environment. LR = little raven. 'Other' indicates retreats by the other combatant species. Other species (number of interactions) that interacted agonistically with LRs were: White-faced heron (1); Straw-necked ibis (3); Tawny frogmouth (1); Masked lapwing (1); Galah (1); Rock dove (1); Laughing kookaburra (1); Red wattlebird (4); Pied currawong (3); Magpie-lark (4); Common starling (1); unidentified raptor (1)

Australian magpies initiated over 90% of their encounters with LRs in both environments. However, the type and outcome differed between the two environments (Fisher P = 0.0002 in both cases) in that magpies predominantly chased

LRs in the U_{env}, but mainly attacked them in the EXU_{env}. This reflected the fact that exurban LRs were likely to 'hold their ground' or flee only a short distance when challenged by magpies, whereas urban LRs predominantly fled > 10 m. There was no significant variation in the types of aggressive encounter observed between LRs and Noisy miners, Common mynas and Australian magpies in the U_{env} ($\chi^2_{(6)}$ = 3.080, P = 0.798), but outcomes varied ($\chi^2_{(6)}$ = 24.800, P< 0.001) (Table **2**). Little ravens mainly retreated > 10 m when challenged by magpies, but < 10 m when confronted by Noisy miners. However, LRs initiated nearly half of their encounters with Common mynas, and fleeing was almost as common an outcome for the mynas as for the ravens in these interactions.

Table 3.   Percentages of types of intraspecific agonistic interactions and encounter outcomes for Little ravens in urban and exurban areas.

Encounters	Urban areas	Exurban areas
Type:		
Approach	38.0	17.7
Threaten	17.6	10.4
Attack	20.1	17.7
Pursue	24.1	50.0
N	108	34
Outcome:		
Retreat > 10 m	39.5	28.2
Retreat < 10 m	57.8	66.7
No retreat	2.8	5.1
n	109	39

n = sample size

Intraspecific Interactions

Intraspecific aggressive interactions were much more common than interspecific interactions in both environments. However, an intraspecific agonistic interaction occurred during 12.9% of first foraging observations (n= 607) of focal LRs in the U_{env} but only during 2.9% in the EXU_{env} (n=1,181) ($\chi^2_{(1)}$ = 66.2, P< 0.001). There was also a significant difference in the types of intraspecific aggressive encounters observed in the two environments (Table **3**). Pursuit was relatively less, and approaching-without-overt threat relatively more common in the U_{env} than the EXU_{env}

Table 4.   **Percentages of Little raven groups of various sizes in the urban and exurban environments during the breeding and non-breeding seasons.**

Group	Environment and Season			
Size	U_{env}	U_{env}	EXU_{env}	EXU_{env}
	breeding	non-breeding	breeding	non-breeding
1	57.9	83.4	71.6	54.2
2	16.3	0.4	17.6	24.8
3	5.5	2.2	4.8	5.2
4	2.3	1.2	1.9	2.5
5	1.1	9.1	1.9	1.2
6-19	1.5	3.1	2.2	7.9
≥ 20	0.1	0.5	1.2	4.0
n	1,036	1,128	809	404

U_{env} and EXU_{env} are urban and exurban environments, respectively.
n = number of observations.

($\chi^2_{(3)} = 9.19$, P = 0.027). However, intraspecific interactions had similar outcomes in the two environments (Fisher exact P = 0.368), with one of the participants retreating < 10 m being the dominant response.

Group Size

The most important finding for group size was that distributions were similar in the U_{env} and EXU_{env}, except that groups of ≥ 20 were recorded about twice as often in the latter environment year-round, but particularly in the non-breeding season (11% versus 6% of sightings) (Table **5**). Ten exurban flocks contained 50-100 individuals, whilst two large flocks of at least 64 and 224 birds, respectively, were recorded in the U_{env}. Overall in the two environments combined, 69% of LR sightings were of single birds, 19% of two birds, 5% of three birds and 1% of ≥ 20 individuals (Table **4**). The Breeding (July-December) and non-breeding season group size distributions were similar, except possibly for the presence of relatively more large groups (≥ 20) in the latter season.

Nest and Nest Site Characteristics

Height, canopy depth and trunk dbh of trees in which nests were built were all significantly correlated, so only tree height was included in the statistical analysis of U_{env}/EXU_{env} nest site disparities. Nest tree characteristics were documented for 8 types of site in U_{env}, particularly roadscapes, gardens and open parkland, and 3 site types in the EXU_{env}, especially roadscapes and paddocks. Little ravens in both environments nested at greater heights in taller nest trees ($r_{(98)} = 0.463$, P<0.01).

The height of LR nests was similar in U_{env} and EXU_{env} ($t_{(98)} = 0.764$, P = 0.447) and the distribution of tree types used for nesting was also similar (Fisher exact P = 0.346; n = 110) (Table **5**). Eucalypts comprised 75% of U_{env} and 83% of EXU_{env} nest trees, respectively. Nest tree height ($t_{(81)} = 1.743$, P = 0.085) and isolation index ($\chi^2_{(3)} = 5.084$, P =

0.166) were also similar in the U_{env} and EXU_{env}. However, nest concealment differed between the two environments ($\chi^2_{(2)} = 12.586$, P= 0.002); the standardized χ^2 residuals were < 2, but they indicated that the almost 2.3-fold greater percentage of very visible nests in the EXU_{env} mainly accounted for the urban-exurban disparity (Table **5** and legend).

DISCUSSION

Diet and Foraging Behaviour

Foraging urban LRs used sealed ground surfaces significantly more than exurban individuals, which was unsurprising given the much greater extent of such substrates in the U_{env}. Exurban individuals used soil substrates for foraging much more than urban con-specifics did, largely due to their tendency to feed in paddocks in which the soil had recently been turned over by farmers. Sweeping occurred at low frequencies in both environments (U_{env} 3.3% and EXU_{env} 5.4% of first foraging records), but it was targeted differently; 65% of exurban sweeping was of residual hay and dry cow faeces, whereas not surprisingly these targets did not feature in the U_{env}. However, apart from these differences, urban and exurban individuals foraged very similarly, mainly by gleaning and probing on grassy substrates, which constituted 91 and 94% of first foraging records in the U_{env} and EXU_{env}, respectively, and probably involved mainly consumption of invertebrates and small plant components, such as seeds. Rowley and Vestjens [28] similarly found that 86% of LR stomachs contained invertebrates and/or plant material and Swinburne and Jessop [32] recorded that insects were prominent in LRs' diet in April on Phillip Island, 139 km from Melbourne. Although the food items obtained by gleaning and probing in the present study might differ in detail in the U_{env} and EXU_{env}, it seems likely that the vast bulk of the urban diet was broadly similar to, and obtained in the same manner as, the bulk of the exurban diet *i.e.* 'pre-adaptation' was evident [18].

Table 5. **Characteristics of nest trees and nests used by Little ravens in the urban and exurban environments.**

Nest/ nest tree variable	Environment		
	Urban	Exurban	Both
Nests:			
Mean ± SE height (m): n *Concealment category (%):*	17.3 ± 0.9 52	18.3 ± 0.9 48	17.8 ± 0.6 100
very visible moderately visible largely hidden	25 60.7 14.3	56.4 40 3.6	
n	53	56	109
Nest trees: *Isolation index (%):*			
0	29.6	13.0	
1-3	46.3	51.8	
4-6	13.0	22.2	
>6	11.1	13.0	
n	54	54	108
Mean ± SE height (m):	22.4 ± 0.7	24.7 ± 1.1	23.5 ± 0.7
n	54	49	103
Mean ± SE canopy depth (m):	18.6 ± 0.7	21.1 ± 1.2	19.8 ± 0.7
n	55	48	103
Mean ± SE trunk dbh (m):	0.7 ± 0.1	1.0 ± 0.1	0.9 ± 0.04
n	43	42	85
Percentage tree type:			
eucalypts	75	83	78
Cupressaceae	21	17	21
Other	4	0	1
n	57	56	113

Standardized χ^2 residuals for nest concealment (urban given first): very visible -1.83 and +1.84; moderately visible +1.08 and -1.09; largely hidden +1.32 and –1.33.

Exurban LRs fed on human food waste using manipulative behaviour, but they did so far less often than urban conspecifics (0.6 *versus* 5.9% of first foraging records), reflecting this resource's relative scarcity in the EXU_{env}. Human food waste was the only identified food item for which there was a clear urban/exurban difference in consumption rate. The behaviour involved was similar in the two environments and thus the motor patterns themselves did not, strictly speaking, constitute innovative *urban* feeding behaviour, but feeding on human food waste generally can be considered innovative [22]. However, although such waste food may be an important resource to the subset of urban LRs that live near shopping centres and food outlets, overall it accounted

for <3% of the species' urban and exurban foraging records. Urban LRs occasionally visit feeding stations provisioned by Melbourne home-owners (Ruwandeniya and Lill, submitted manuscript), but whether these artificial food sources are very important in their diet is unclear.

Although invertebrates and detached plant components apparently comprised >90% of the diet in both environments, the LR was an opportunistic dietary generalist in both the U_{env} and the EXU_{env} in that its diet encompassed both natural foods (living invertebrates, vertebrate carrion, seeds, fruit and nectar) and artificial foods (human food waste and stock food). Being an ecological generalist is thought to facilitate successful urban colonization, because the novel conditions encountered in cities are more likely to be encompassed by the environmental tolerance range exhibited by such species, which is broader than that of ecological specialists [23, 33].

Foraging Competition

Foraging Little ravens spent only a small percentage of their time close to other bird species in both the U_{env} and EXU_{env} (9% and 7%, respectively). Most of this time was spent near to just two species in each environment, the Common myna and Common starling in the U_{env} and the Australian magpie and Common starling in the $EXU_{env.}$ Some other native species that forage in both environments in similar habitats and on similar substrates to LRs (e.g. the Magpie-lark) rarely fed close to them. Thus conceivably, foraging LRs were avoided by, or avoided foraging close to, some native bird species that have some dietary overlap with them (i.e. possible food resource partitioning occurred [34].

During the entire study and across both environments, foraging LRs had more than 5 interspecific agonistic interactions with only three bird species and the overall mean interspecific agonistic interaction rate (interactions per foraging raven observed) was 0.034. Although the 'currency' was different, the mean urban rate (0.023) was as low as those of several other bird species in urban Melbourne [35-37]. Interspecific agonistic interactions between LRs and urban Noisy miners and Australian magpies were mainly initiated by the latter species and were mostly of high intensity, 89-95% being attacks and chases. They resulted in displacement of urban ravens >10 m on 61-70% of occasions, but the ravens usually then resumed foraging. However, LRs initiated the aggression in nearly half of their encounters with Common mynas and elicited retreat, mostly >10 m, in one third of them. Nonetheless, overall there was little persuasive evidence of a substantial level of aggressive interference competition for food between urban or exurban LRs and cohabiting bird species. This finding intriguingly mirrors the lack of such competition between introduced and native bird species globally [38].

Intraspecific agonistic interactions were 4.5 times more common in the U_{env} than the EXU_{env}, despite large flocks apparently being more common in the latter environment in the non-breeding season. This trend may reflect a higher population density in the city, as has been demonstrated for other urban-colonizing bird species [17]. The urban interactions were also less escalated, only 44% being attacks and pursuits compared with 68% in the EXU_{env}. This could indi-

cate that a greater level of intraspecific tolerance is advantageous for LRs living at higher densities. However, on average, U_{env} and EXU_{env} interactions had similar outcomes, the 'loser' mostly retreating for just a short distance with minimal disruption to its foraging. Thus although intraspecific agonistic interactions were 3.5 times more frequent than interspecific ones, their probable cost to the participants appeared mostly to be relatively low.

Group Size

Avian flocking can have anti-predation and/or food-finding and exploitation benefits and has been proposed as a trait facilitating urban colonization [18]. However, the one convincing difference between the U_{env} and EXU_{env} in LR group sizes, even in the absence of significance testing, was the occurrence of proportionally more large flocks in the EXU_{env}, especially in the non-breeding season. Moreover, in both environments most LRs observed were single birds or in pairs (88% of all records) and flocks of 20 or more constituted just 2.2% of all sightings, so flocking was not a major phenomenon other than at nocturnal roosts. These findings are not consistent with flocking being a major facilitator of urban colonization by LRs. Duncan *et al.* [39] reached a parallel conclusion about colonization of Australia generally by introduced bird species. Swinburne and Jessop [32] found that gregarious behaviour was more common in LRs in mainly EXU_{env} on Phillip Island than in our study, but their investigation was restricted to autumn and encompassed just three sites.

Flocking could potentially have some role in urban colonization by LRs through facilitating social learning about novel urban food sources, such as human food waste. Ten percent of large exurban flocks were feeding on recently-turned soil or under concentrations of dry cow faeces in paddocks, which clearly presented a rich, localised food source, but the rest were in grassy paddocks or roadscapes whose relative food abundance was unknown. Our observations suggested that LRs, especially in the U_{env}, were not as nomadic or gregarious outside the breeding season as Rowley [30] suggested.

Theoretically, food-finding may actually be less problematic in the U_{env} than the EXU_{env} because of the greater food abundance in the former environment. However, urban colonizer population densities, and hence probably intraspecific food competition levels, may also be higher in the U_{env} [6], as observed in the LR. Relative predation pressures on birds in the two environments are even less clear-cut. Some authors argue that they are lower in cities because of a reduced density of natural predators [40] and even that the U_{env} may act as a refuge from natural predators by virtue of the high level of human presence [41]. Other authors suggest that the alleged lower urban natural predator density is more than compensated for by the high abundance of mesopredators [42]. However, adult LRs' large body size may mean that they have relatively few natural predators anyway, other than raptors. Their eggs and nestlings may be more vulnerable than they are in both environments.

Nests and Nest Sites

There were no disparities in nest tree type, size or isolation between the U_{env} and $EXU_{env.}$ Thus LRs appeared to be 'pre-adapted' for nesting in the U_{env}. Nests were mostly only moderately hidden by foliage, but urban nests were more concealed than exurban nests. As there were no obvious systematic differences in tree canopy density between the U_{env} and EXU_{env}, this possibly indicated that nest predation risk was greater in the city.

Typically, nests were built in eucalypts or cypresses/cypress-pines ~24 m tall, with a canopy 20 m deep. There were usually 1-3 nearby trees of similar height that might potentially have provided concealment for nest predators. Two reasons for the predominant choice of eucalypts as nest trees could be that they are: (a) the most common of Melbourne's street trees [43] and also very common in rural Victoria, and (b) mostly quite tall. Little ravens nested higher above ground level in taller nest trees, which could possibly have reduced the risk of predation of young that were being reared in large, mostly only moderately concealed nests. However, the second most frequently used nest trees were cypresses and cypress-pines, which are also tall but only the eleventh most common of Melbourne's street trees [43]. Therefore, unidentified factors other than relative abundance and height were probably partly responsible for the predominance of eucalypts as nest trees for both urban and exurban LRs.

FUTURE RESEARCH

Little ravens probably first colonized Melbourne extensively in the 1980s [44] and 30 years later are widespread and abundant in the city. Future studies of the foraging ecology, nesting behaviour and sociality of this recent urban colonizer could profitably extend sampling to more than one non-breeding season, more than one major conurbation and to dry sclerophyll eucalypt forest in the EXU_{env}. It would also be helpful in understanding the LR's success in colonizing cities to determine whether its population density really is higher in the U_{env} than the EXU_{env} and examine in more detail possible niche partitioning with other urban bird species.

LIST OF ABBREVIATIONS

EXU_{env}	=	Exurban environment
LR	=	Little raven
U_{env}	=	Urban environment

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

PATIENT'S CONSENT

Declared none.

APPENDIX 1

Scientific names of species mentioned in text. Total lengths (cm) sourced from [45] are given for the bird species in parentheses.

Birds:

Australian magpie *Cracticus tibicen* (38-44)

Common blackbird *Turdus merula* (25-26)

Common myna *Acridotheres tristis* (23-25)

Common starling *Sturnus vulgaris* (21)

Eucalypts, genera *Eucalyptus*, *Corymbia* and *Angophora*.

Galah *Cacatua roseicapilla* (34-38)

Grey butcherbird *Cracticus torquatus* (24-30)

House mouse *Mus musculus*

Laughing kookaburra *Dacelo gigas* (41-47)

Magpie-lark *Grallina cyanoleuca* (26-30)

Mammals:

Masked lapwing *Vanellus miles* (35-38)

Noisy miner *Manorina melanocephala* (24-27)

Pied currawong *Strepera graculina* (42-50)

Plants:

Red wattlebird *Anthochaera carunculata* (33-36)

Rock dove *Columba livia* (33-36)

Silky oak *Grevillea robusta*

Straw-necked ibis *Threskiornis spinicollis* (58-76)

Sulphur-crested cockatoo *Cacatua galerita* (44-51)

Tawny frogmouth *Podargus strigoides* (33-50)

Cupressaceae – cypress-pine *Callitris*, cypress *Cupressus* and *Actinostrobus*

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