

Foraging of Sulphur-crested Cockatoos: examining the roles of preadaptation, behavioural flexibility and interspecific competition in urban dwelling

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Some birds must adjust their ecology to colonize cities, whilst others are more inherently suited for urban life. Large parrots with neuron-rich brains and high cognition levels might be predicted to have the plasticity to exploit novel urban resources through innovative behavioural adjustments. Sulphur-crested Cockatoos *Cacatua galerita* have colonised many Australian cities, but their urban ecology is only now becoming known. We investigated their foraging in Melbourne to elucidate whether the species' synurbanization has involved ecological and behavioural adjustments in this activity, and whether interspecific interference competition is involved in food acquisition. Sixty-one percent of urban foraging flocks contained 1-10 members and the largest flock comprised 42 individuals. The diet comprised mainly grass seeds and roots (54%), bulbs and corms (22%) and tree fruits, inflorescences and seeds (22%). Supplementary, anthropogenic food was consumed infrequently and no innovative foraging behaviour with respect to such novel foods occurred. Gleaning and digging on grass comprised 68%, and arboreal feeding ~22%, of foraging behaviour. Feeding ecology mostly resembled that of nonurban conspecifics, except that in cropland the latter extensively exploit cereal crops using seed-head gleaning and stalk felling. Collectively, various heterospecific birds were close to foraging cockatoos for ~50% of the time, including other cockatoos. However, these close relatives spent only a limited time near Sulphur-crested Cockatoos, and only Long-billed Corellas *C. tenuirostris* had a significant, although small, agonistic involvement with them. Although 90% of these agonistic interactions caused Sulphur-crested Cockatoo displacement, the distance and duration were usually short and the cockatoo's foraging efficiency was minimally impaired. We concluded that Sulphur-crested Cockatoos: (a) are substantially preadapted for foraging in Melbourne, exhibiting few pronounced adjustments for urban life in this respect; innovative foraging techniques reported elsewhere appear to be either rare or have not yet arisen in Melbourne, and (b) mostly did not engage in obvious interspecific interference competition with other bird species to acquire food.

Keywords: cockatoo; synurbanization; diet; foraging behaviour; preadaptation; interspecific competition.

INTRODUCTION

A central issue in urban ecology is how some animal species can colonize and thrive in cities (urban exploiters and adapters) whilst others cannot (urban avoiders) (Blair 1996). It is thought that successful urban colonization can be influenced by, *inter alia*, behavioural plasticity, the tendency to forage gregariously and interspecific interference competition (Mills *et al.* 1989; Sol *et al.* 2013; Martin and Bonier 2018).

Cities often contain abundant food resources in the form of deliberately provided supplementary food (e.g. seed, bread or meat at garden feeders) and incidental human food waste (e.g. 'left overs' in garbage bins) (Lill and Hales 2015; Jones 2018). Whilst supplementary food often requires little behavioural adjustment to exploit effectively (Sol *et al.* 2013), some human waste food can only be accessed through technical innovation and problem-solving, sometimes enhanced by social learning (e.g. Webster and Lefevbre 2001; Bouchard *et al.* 2007). The level of cognition required for such behaviour reflects the absolute number and distribution of cerebral neurons (Herculano-Houzel 2011; Olkowicz *et al.* 2016). Thus, birds which have high brain neuron counts and a relatively large forebrain should be advantaged when innovative behaviour is necessary to access novel food resources in cities.

Large parrots are long-lived, highly intelligent, continually learning and adept at cognitive feats (Huber and Gajdon 2006; Auersperg *et al.* 2012). Their great cognitive ability reflects their high brain neuron densities and the high percentage of these neurons that are in the forebrain (the centre of intelligence) (Olkowicz *et al.* 2016). The Sulphur-crested Cockatoo *Cacatua galerita* (SCC) weighs 600-1000 g; its brain weighs just 10 g but contains ~2 billion neurons, far more than the comparably-sized brains of some mammals (Olkowicz *et al.* 2016). In captivity, it performs some discrimination and insight tasks with a high success rate (Magat and Brown 2009; Krashenninnikova *et al.* 2013).

Over the last 40-50 years SCCs have successfully colonized many conurbations throughout their Australian range. However, their urban ecology is only just starting to become better known, with the most detailed published studies of their ecology still being those conducted last century in nonurban areas (Noske 1980; Emison and Nichols 1992). Given its 'neuron-rich' brain, the SCC might be predicted to have the behavioural flexibility to exploit novel urban resources, such as human food waste, using innovative behaviours. Indeed, an ongoing Sydney study of which we became aware during the present investigation has documented at least two examples of such innovation (wheelie bin raiding and sprinkler drinking) (Jones 2019). There is,

however, increasing recognition that urban colonizing animals are also to some extent preadapted to city conditions (Van Heezik *et al.* 2008; Sol *et al.* 2013; McDonnell and Hahs 2015; Clifton and Jones 2017; Masicovetere and Lill 2018; Rakhimov and Ibragimova 2018) and this could be true of aspects of the SCC's foraging ecology, given that components of its nonurban diet are present in cities (Higgins *et al.* 1999).

It has been hypothesised that foraging gregariously may facilitate successful urban colonization and persistence (Mills *et al.* 1989; Duncan *et al.* 2003). It is adaptive in many birds for various reasons, including finding and efficiently using food, reducing predation risk, overcoming competition, reducing neophobia in novel feeding situations and using innovative problem-solving (Coleman and Mellgren 1994; Kark *et al.* 2006; Liker and Bokony 2009; Beauchamp 2015; Evans *et al.* 2016). In accordance with the urbanization hypothesis, Kark *et al.* (2006) demonstrated that inner city 'urban exploiter' birds are more social than suburban 'urban adapters' and that avian sociality is correlated with the degree of urbanization of the environment in Jerusalem, Israel.

Interspecific interference competition may influence which species can persist or thrive in cities (Sol *et al.* 2012, 2013; Martin and Bonier 2018). Aggressive interactions are very common among closely related species and can be instrumental in interference competition for resources, which can affect species' coexistence (Amarasekare 2002; Peiman and Robinson 2010; Dhondt 2012; Ferry *et al.* 2016). Urban colonizers can acquire resources either by aggressively displacing resident competitor species from those resources or by exploiting resources infrequently used by residents (Tilman 2004). In most interspecific interference competition one of the competing species is always dominant and the other always subordinate (Martin *et al.* 2017). Dominant species may be better equipped to persist when the urban environment contains many resources that can be aggressively monopolized (e.g. novel resources, such as human food waste); subordinate species may be more likely to persist when the urban environment is more challenging (e.g. low resource levels) because they are often excluded from preferred resources and may therefore be better adapted to challenging conditions. However, the influence of interference competition on the responses of native species to urbanization has not been widely investigated, although we know that competitiveness co-varies with boldness and environmental tolerance, which are important in urban adjustment (Martin and Bonier 2018).

This investigation had two underlying rationales:

- (1) to facilitate comparison of the SCC's urban feeding ecology with that of nonurban conspecifics to assess the extent to which synurbanization (adjustment to the urban environment) has involved behavioural and ecological modifications promoting urban food acquisition. This was achieved by documenting the following features of urban SCCs' feeding ecology and comparing them with those of nonurban conspecifics as reported in the literature: (a) the diet, in terms of the plant species and food items exploited, and (b) foraging behaviour, substrate use and group sizes.
- (2) to assess whether urban SCCs must engage in interspecific interference competition to obtain food. This was achieved by documenting which bird species occurred close to

foraging SCCs and the extent and outcome of agonistic interaction between these heterospecifics and the cockatoos.

This study of SCCs forms part of an investigation of synurbanization in four cockatoo (Cacatuidae) species in Melbourne, south east Australia, the other species being the Galah *Cacatua roseicapillus* (Lill and Polley 2020), Little Corella *C. sanguinea* and Long-billed Corella *C. tenuirostris* (Polley and Lill 2020).

METHODS

Study species, area and timing

The SCC mainly inhabits northern and eastern Australia in many natural and modified habitats, including tropical swamps, *Eucalyptus* forests, semi-arid woodlands and treed farmland. It mostly forages gregariously on the ground, but also to a limited extent in trees and shrubs. It consumes a variety of natural food items including seeds, fruits, inflorescences, bulbs, corms and insect larvae; however, it also exploits cereal and oilseed crops, and orchard fruits and nuts, which has gained it pest status in some quarters (Higgins *et al.* 1999).

Our investigation was conducted in urban Melbourne (area ~10,000 km²; human population just over 4 million) from early autumn to late winter (March to August), 2019, the SCC's non-breeding season. Mean maximal and minimal daily ambient temperatures ranged from 14.5°C (August) to 24.8°C (March) and 7.4°C (August) to 15.2°C (March), respectively. Monthly precipitation varied from 7.2 mm (April) to 53.4 mm (May). The foraging sites at which observations were made were widely dispersed throughout urban Melbourne (Fig. 1). Observations of foraging were mostly made reasonably close to roost sites in the early morning and late afternoon because these gregarious birds were difficult to find consistently during the middle of the day. However, accounts for nonurban areas indicate that these are the times at which more foraging occurs anyway (Noske 1980).

Diet

Representative samples of the food plants exploited by urban SCCs were collected, preserved and identified. It would have been impossible to quantify the entire diet in terms of every food plant exploited by every focal cockatoo in every foraging event. Instead we documented the main types and genera of food plants used, their relative importance in the diet and which components of these plants were exploited. Identification of plants was undertaken with the aid of expert opinion, and written sources including the Australian National Herbarium and Agriculture Victoria plant and weed lists.

Foraging behaviour

Observations of foraging behaviour were made from a vehicle and on foot. To reduce pseudoreplication and yet obtain a large, representative sample, we adopted the following protocol:

1. The maximum number of foraging records collected per focal individual was five and the maximum number of records per flock was twenty-five.
2. Flocks had to be at least 50 m apart, without frequent exchange of members.

3. Sites at which observations were made were not re-used until at least 42 days had elapsed.

When foraging SCCs were in a flock, focal individuals were chosen according to a consistent set of arbitrary rules and had to be at least 20 m apart. For each focal foraging cockatoo, we used 10 × 42 power binoculars to assist in recording:

- (A) the substrate on which the bird was standing or perching: (i) bare soil, (ii) grass, (iii) sealed surfaces (e.g. bitumen, concrete), (iv) leaf litter, and (v) tree branch or twig. The substrate from which the food item was obtained was usually that on which the focal foraging individual was standing or perching.

- (B) foraging behaviour used:

1. Gleaning – picking food items off the substrate with the beak, usually in a single movement:

- (a) Ground gleaning (GG) – gleaning on the ground.
 (b) Ground gleaning with beak (GGBM) or foot manipulation (GGFM) of the food item – as for (a), but the food item noticeably held/manipulated in the beak or the foot prior to ingestion.
 (c) Perching gleaning – Upright (PGU) or – Leaning (PGL) – gleaning conducted while perching on vegetation either upright or leaning out to the food source.

- (d) Perching gleaning with either beak (PGBM) or foot manipulation (PGFM) of the food item – gleaning while perching on vegetation, but using either the beak or the foot to hold/manipulate the food item before ingestion.

- (e) Perching gleaning – Inverted (PGI) – gleaning on vegetation while hanging upside down.

2. Digging (D): Digging into the soil with the beak, shoveling ground-covering vegetation and soil away:

- (a) Digging with the beak (D).
 (b) Digging with foot manipulation (DFM) of the food item – as for (D), but the food item is manipulated/held in the foot before/during consumption.

3. Probing (Pr): making *repeated* penetrating probes into vegetation with the beak:

- (a) Ground probing (GP) – conducted on the ground by repeatedly probing into ground cover vegetation before picking up the food item with the beak.
 (b) Ground probing with beak manipulation (GPBM) – as for (f), but the food item is manipulated/held in the beak before ingestion.

4. Prise: lever off bits of tree bark with the beak.

- (C) habitat in which foraging occurred:

Wooded parkland, parkland, sports field, streetscape, garden, golf course, school grounds, open grassy area and carpark. These categories are largely self-evident and have been described by Lill and Polley (2020).

Foraging flock size

It was often impossible to establish the exact size of large, dynamic foraging flocks. Therefore, the size of all foraging flocks encountered during the study was recorded categorically in units of five, but with the highest category being >40.

Data analysis

Chi-squared tests of independence (sometimes with some category pooling) were used to test for seasonal differences in diet, foraging behaviour and flock size. Where significant chi-squared values were obtained ($\alpha = 0.05$), examination of standardised residuals (*SR*) was used to help determine exactly where the differences occurred (Sharpe 2015). A more refined temporal analysis than a simple autumn versus winter split would have been desirable, but would have required sampling a constant suite of sites regularly throughout the study period, which was precluded by the emphasis on obtaining spatially representative samples.

The foraging behaviour profile and the foraging substrate use profile were similar whether all records were included or only arbitrarily the last behaviour in each sequence of at least five from a foraging flock. Therefore, the summaries presented are based on the entire data sets.

RESULTS

Sightings and foraging flock sizes

Sightings of SCCs were obtained from 82 locations from ~1 to ~80 km apart throughout urban Melbourne (Fig. 1). The SCC foraging flock size distribution differed between autumn and winter ($\chi^2_{(5)} = 24.548$, $P < 0.001$, with some combining of categories) (Fig. 2). The chi square residuals indicated that this difference was due to there being relatively more flocks of 11-15 members (*SR* 3.254) and relatively fewer flocks of > 26 members (*SR* -2.834) in autumn than winter. The most common foraging flock size category was 1-5 members (41% of the 80 foraging flocks), 20% of flocks contained 6-10 members and the largest foraging flock comprised 42 individuals.

Diet

If the total number of SCCs observed feeding on a specific food item is considered, 227 individual dietary items of urban SCCs were identified (84 in autumn, 143 winter), belonging to six broad categories: (1) attached and detached grass seeds and roots (54% of records), (2) bulbs and corms, mainly of Onion Grass *Romulea rosea* (22%), (3) tree and shrub fruits, flowers and seeds, mainly *Eucalyptus* seeds (22%), (4) herb seeds, flowers and leaves (2%), (5) *Eucalyptus* bark and (6) anthropogenic foods (each <1%). Overall, the relative consumption of the three most frequently eaten food items (grass seeds/roots, bulbs/corms and tree seeds/flowers) was similar in the two main foraging habitats used (streetscapes and parkland), and did not vary seasonally ($\chi^2_{(2)} = 2.613$, $P > 0.05$) (Table 1).

Twenty-eight specific sources of dietary items were identified: five grass (Poaceae) species or genera (seeds and roots), six herb species in five families (seeds, inflorescences and leaves), 17 tree and shrub genera in 12 families (fruit, seeds, nuts, inflorescences and bulbs) and five anthropogenic sources

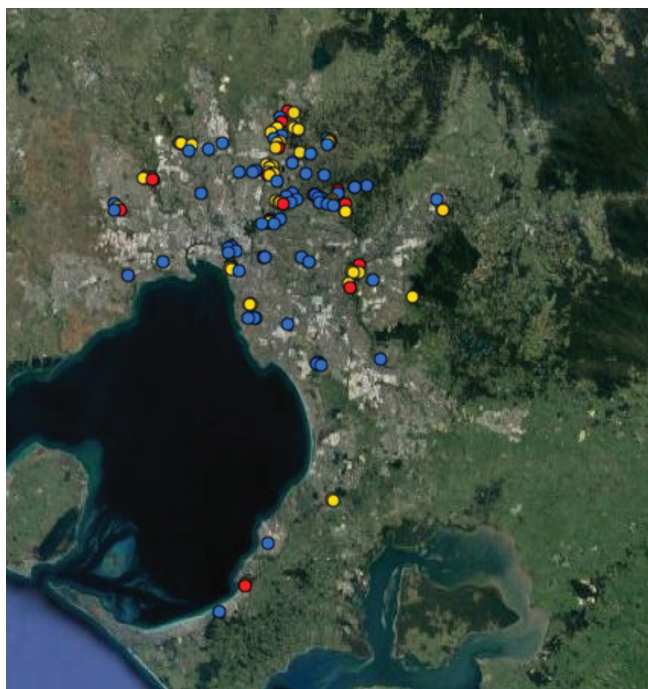


Figure 1. Sightings of Sulphur-crested Cockatoos in urban Melbourne. The image covers an area of 103 km (width) x 109 km (depth); dark coloured area of water is Port Phillip. Filled circles indicate: sighting locations only = blue; sighting and foraging locations = yellow; known roost locations = red.

(Table 2). All but two of the plant genera (*Eucalyptus* and *Melaleuca*) were exotic. The anthropogenic items consumed were food deliberately fed to the cockatoos by one person at one location and discarded waste food items consumed at several locations.

Foraging behaviour

The five foraging habitats were utilised at widely varying frequencies overall (Fig. 3), but there was no seasonal variation in the relative use of habitats ($\chi^2_{(4)} = 3.090, P>0.05$). Foraging behaviour records (n=227) were obtained on 80 occasions from 28 locations, primarily streetscapes (46% of autumn records; 50% of winter records) and parkland (29% autumn; 32% winter). The three main foraging behaviours were gleaning, digging and probing, which had respectively eight, two and three variants (Fig. 4a). Ground-based gleaning and digging were the most common foraging behaviours, together accounting for ~68% of foraging behaviour, whilst arboreal foraging comprised 22% of the repertoire (Fig. 4b). Ground-based probing accounted for <9% of foraging behaviour and all the other foraging behaviours occurred infrequently. Use of the foot to hold or pin down a food item was quite common, occurring in 18% of foraging behaviours. The foraging behaviour profile varied seasonally ($\chi^2_{(13)} = 31.420, P<0.01$) (Fig. 3); the chi square residuals indicated that this was due mainly to a large relative increase in digging in winter (SR 5.7).

Not surprisingly, given the predominance of ground-based gleaning and digging, grass was the dominant foraging substrate used in both seasons, accounting for 71% of foraging substrate used in both seasons, accounting for 71% of foraging substrate use overall. Twigs and branches accounted for 23% of usage

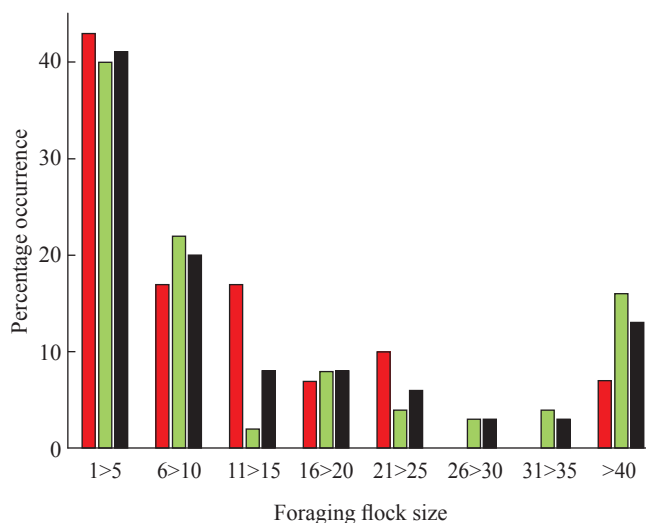


Figure 2. Overall and seasonal foraging flock size distributions of urban Sulphur-crested Cockatoos. Autumn = red; winter = green; overall = black. There were no flocks comprising 36-40 cockatoos.

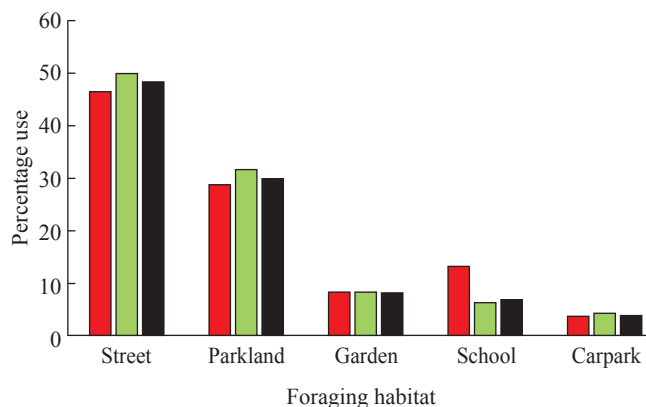


Figure 3. Observed overall and seasonal percentage usage of main foraging habitats by urban Sulphur-crested Cockatoos. Autumn = red; winter = green; overall = black.

Table 1

Percentage consumption by urban Sulphur-crested Cockatoos of their three main food types in their two main foraging habitats. A = autumn, W = winter and O = overall (bold font). n = number of observations.

Habitat	Season (n)	Grass seeds/ roots	Bulbs/ corms	Tree Seeds/ Flowers
Streetscape	A (39)	71.8	12.8	15.4
	W (71)	46.5	25.4	28.2
	O (110)	55.5	20.9	23.6
Parkland	A (23)	73.9	17.4	8.7
	W (45)	71.1	15.6	13.3
	O (68)	72.1	16.2	11.8

(Fig. 5), whilst bare soil and sealed surfaces were only utilised at low frequencies. Foraging substrate use appeared to vary seasonally, with greater bare soil and sealed surface usage in autumn than winter, and greater grass and twig and branch usage in winter than in autumn (Fig. 5).

Table 2

Plant species and anthropogenic items that provided components of urban Sulphur-crested Cockatoos' diet. The listing is alphabetical within categories. The label 'sp.' indicates that the species was unidentified but known not to be any other species in this listing. ⁰ indicates identified qualitatively as food plant but not incorporated in overall quantitative diet composition. * indicates that the plant genus has been recorded in the SCC's diet elsewhere. Higgins *et al.* (2001) list a lot of additional genera reported as food plants of SCCs at some time of year (including some New Zealand records).

Species	Component(s) consumed
Grasses (Poaceae):	
<i>Paspalum dilatatum</i> Paspalum	root, seed
<i>Pennisetum clandestinum</i> Kikuyu Grass	root, seed
<i>Poa annua</i> Annual Meadow Grass	root, seed
<i>P. bulbosa</i> Bulbous Bluegrass	root, seed
<i>Poa</i> sp.	root, seed
Herbaceous plants:	
* <i>Arctotheca calendula</i> (Asteraceae) Capeweed	root, leaf, inflorescence
<i>Oxalis pes-caprae</i> (Oxalidaceae) Bermuda buttercup	root, inflorescence, seed
* <i>Plantago coronopus</i> (Plantaginaceae) Plantain	seed
* <i>Romulea rosea</i> (Iridaceae) Onion grass	corm, root
<i>Rumex</i> sp. (Polygonaceae) Dock	root, leaf
* <i>Taraxacum</i> sp. (Asteraceae) Dandelion	inflorescence, leaf
Trees and shrubs:	
* <i>Citrus x sinensis</i> (Rutaceae) Orange	fruit
<i>Cotoneaster</i> sp. (Rosaceae) Cotoneaster	fruit
* <i>Eucalyptus</i> sp. (Myrtaceae) Eucalypt	fruit, nut
<i>E. camaldulensis</i> River Red Gum	inflorescence, nut
<i>E. leucoxylon</i> Yellow Gum	inflorescence, nut
<i>E. ovata</i> Swamp Gum	inflorescence, nut
<i>E. viminalis</i> Manna Gum	inflorescence, nut
<i>Grevillea robusta</i> (Proteaceae) Silky Oak	seed
⁰ <i>Kolreuteria</i> sp. (Sapindaceae) Golden Rain Tree	seed
<i>Magnolia</i> sp. (x <i>soulangeana</i>) (Magnoliaceae) Magnolia	seed
<i>Melaleuca</i> sp. (Myrtaceae) Paperbark	inflorescence
* <i>Olea</i> sp. (Oleaceae) Olive	fruit
* <i>Pinus</i> sp. (Pinaceae) Pine	needle
* <i>Platanus x acerifolia</i> (Platanaceae) London Plane	seed
⁰ <i>Protea</i> sp. (Proteaceae) Protea	inflorescence
* <i>Prunus</i> sp. (Amygdaloideae) Cherry	fruit
* <i>Quercus</i> sp. (Fagaceae) Oak	nut (acorn)
Anthropogenic:	
Bread	
Biscuits	
Processed oats	
Processed rice	
Seed mix	

Interspecific association and agonistic interaction

Heterospecific birds were within 10 m of focal foraging SCCs 61% of the time. Seven species were involved, but the Long-billed Corella and Little Corella were the only ones exhibiting this proximity frequently (Table 3). Interspecific

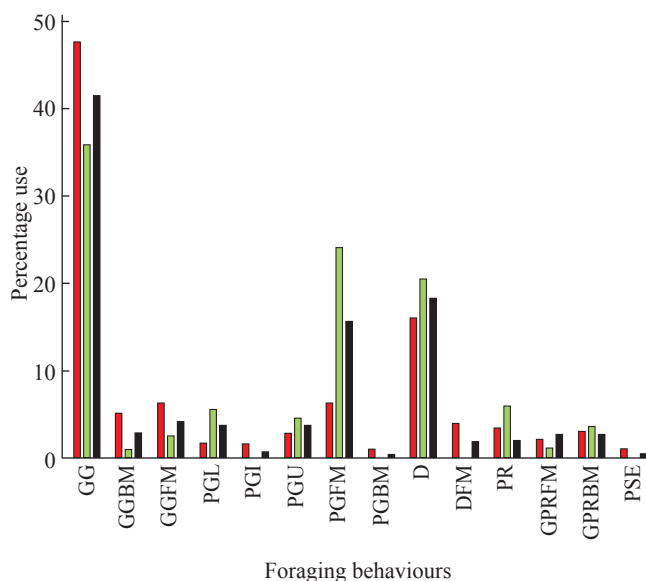


Figure 4a. Overall and seasonal percentage composition of the full foraging behaviour repertoire of urban Sulphur-crested Cockatoos. Abbreviations are GG = ground gleaning, GGBM= ground gleaning with beak manipulation, GGF= ground gleaning with foot manipulation, PGL= perching gleaning-leaning, PGI = perching gleaning inverted, PGU= perching gleaning-upright, PGFM= perching gleaning with foot manipulation, PGBM= perching gleaning with beak manipulation, D= digging, DFM = digging with foot manipulation, GPRFM= ground probing with foot manipulation, GPRBM = ground probing with beak manipulation and PSE = prising. See Methods for descriptions of these behaviours. Autumn = red; winter = green; overall = black.

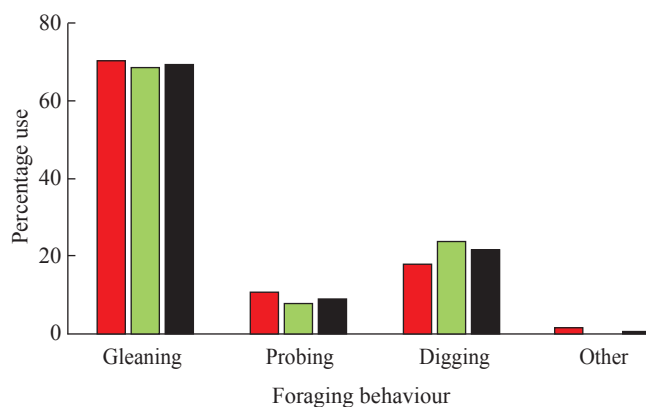


Figure 4b. Overall and seasonal percentage composition of the 'condensed' foraging behaviour repertoire of urban Sulphur-crested Cockatoos. Autumn = red; winter = green; overall = black.

agonistic interactions with foraging SCCs took place during just 14% of these proximity situations; they involved only five species, with the Long-billed Corella being the predominant one. The interactions were initiated by the heterospecific bird on 84% of occasions, initiation involving approaching, threatening or attacking. All five of the heterospecific species involved in these agonistic interactions caused spatial displacement of the foraging SCCs but only the Long-billed Corella did so commonly. Displacement was usually only for a short distance and short duration.

Table 3

Percentage occurrence of bird species near foraging Sulphur-crested Cockatoos and their involvement in agonistic behaviour with, and in displacing, them. Column 2 shows percentage of all occurrences of species near foraging Sulphur-crested Cockatoos; column 3 shows percentage involvement in observed agonistic behaviour with foraging Sulphur-crested Cockatoos; column 4 gives percentage of involvements in which species displaced foraging Sulphur-crested Cockatoo(s). Species listed in order of how commonly they occurred within 10 m of foraging Sulphur-crested Cockatoos.

Species	Occurrence within 10 m of Sulphur-crested Cockatoo(s)	Involvement in agonistic behaviour with Sulphur-crested Cockatoo(s)	Displacement of Sulphur-crested Cockatoos(s)
Long-billed Corella			
<i>Cacatua tenuirostris</i> (500-650 g)	10.6	16.7	91.7
Little Corella			
<i>Cacatua sanguinea</i> (350-660 g)	6.2	0	0
Noisy Miner			
<i>Manorina melanocephala</i> (55-64 g)	1.3	11.1	100
Galah			
<i>Cacatua roseicapillus</i> (255-430 g)	0.9	66.7	25
Australian Magpie			
<i>Cracticus tibicen</i> (220-360 g)	0.4	33.3	100
Little Raven			
<i>Corvus mellori</i> (425-650 g)	0.4	33.3	100
Little Wattlebird			
<i>Anthochaera chrysoptera</i> (45-85 g)	0.4	0	0

SYNTHESIS AND DISCUSSION

Foraging flock size

Few bird species exhibit a dramatic change in foraging sociality when they colonize cities (Sol *et al.* 2013). Non-breeding SCCs in Melbourne mostly foraged gregariously like nonurban conspecifics (Noske 1980; Emison and Nicholls 1992; Higgins *et al.* 1999), so they should be able to exploit some of the proven advantages of social foraging in birds (Kark *et al.* 2006)

Sulphur-crested Cockatoos were widely distributed throughout urban Melbourne. The most common foraging flock size of urban SCCs was 1-5, 61% of foraging flocks comprised ≤ 10 cockatoos and maximum flock size was 42. Foraging flock sizes for nonurban SCCs reported in the literature are:

- A. mainly Victoria (agricultural land) – means: autumn ~53, winter ~35 (Emison and Nichols 1992).
- B. north-eastern New South Wales (mixed farming and cropland) – monthly means: autumn 20-58, winter 22-55;

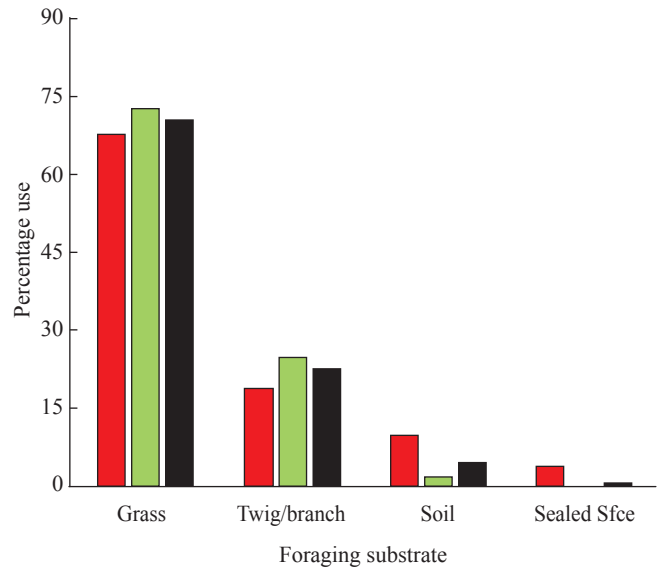


Figure 5. Overall and seasonal percentage usage of foraging substrates by urban Sulphur-crested Cockatoos. Autumn = red; winter = green; overall = black. Sfce = surface.

monthly maxima: autumn 70-150, winter 120-150; most common size category 1-5 (Noske 1980).

The data for nonurban environments are limited, but it appears that in the non-breeding season maximum foraging flock size was larger in nonurban areas than in Melbourne in our study (Table 4). The related Galah, Little Corella and Long-billed Corella exhibit similar trends (Lill and Polley 2020; Polley and Lill 2020). The disparity in foraging flock size is probably associated with food abundance and dispersion. Emison *et al.* (1994) noted that the related Long-billed Corella in cropland in winter congregated in large numbers on spatio-temporally concentrated, but transitory, food sources, such as germinating cereal and mature sunflower (*Helianthus*) crops. The large congregations eventuated because small flocks and individual birds flew to join conspecifics that they had observed feeding on a superabundant food source. Just over half the diet of urban SCCs in winter comprised the seeds and roots of regularly mown turf grasses in streets and parkland. Whilst the presence of a foraging flock at such a resource may still attract other conspecifics to join it, it seems unlikely that this abundant, but less transient and more widely dispersed, food resource would often stimulate the aggregation of as many birds as congregate at rural cereal crop sites. If this speculation is correct, it does not preclude the possibility that flock foraging may have anti-predation benefits for urban SCCs.

Diet

Attached and detached seeds and roots of exotic grasses were the most common item in urban SCCs’ diet. As some of these grasses are rhizomatous, their roots should constitute a high-quality food source (Dong and de Kroon 1994). This dietary component was obtained mainly from regularly mown turf grasses planted in street nature and median strips and in parkland. It was mainly acquired by standing on the grass and gleaming. Bulbs and corms, which comprised 22% of the diet overall, were acquired mainly from the same micro-and

Table 4

Summary of foraging ecology and behaviour of urban and nonurban Sulphur-crested Cockatoos. Sources for nonurban information are Noske (1980), Emison and Nichols (1992) and Higgins *et al.* (1999).

Variable	Urban	Nonurban
Flock size	Main category: 1-5 Maximum: 42	Main category: 1-5 Maximum: 35-58 70-150
Diet	Main items: grass seeds and roots; bulbs and corms; tree seeds, flowers, fruit Minor items: herb seeds, flowers, roots, leaves; supplementary food (bread, processed cereal, commercial seed mixture)	Main items: cereal and oilseed grains; grass seeds and roots; bulbs and corms; tree seeds and fruit Minor items: herb seeds, roots and fruit; supplementary food (cereal grain in trails, storage and spillages)
Behaviour	Main types: ground-gleaning; digging; tree-gleaning Minor types: probing; prising	Main types: ground-gleaning; digging; seed-head gleaning; stalk 'felling' Minor types: tree-gleaning; probing; faecal sorting

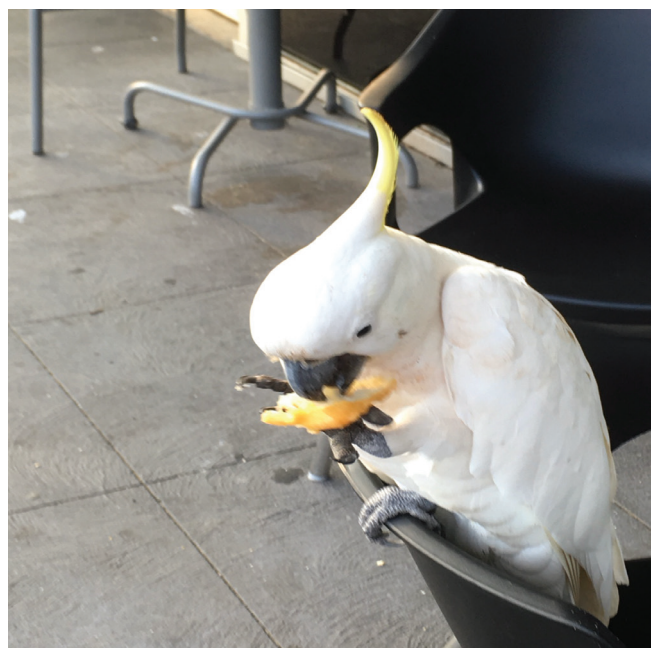


Figure 6. A wild Sulphur-crested Cockatoo eating its daily ration of potato chips at a Melbourne café (photo courtesy S. Bowen).

macro-habitats as grass components and by standing on grass substrates, but digging with the beak was the harvesting method. The third major dietary component, seeds and inflorescences of trees (particularly eucalypts), was obtained mainly by perching on branches and twigs and gleaning in various postures. Thus, gleaning and digging dominated the foraging behaviour repertoire. Use of a foot to hold the food item would mostly not have been appropriate or helpful when feeding on grass and herb seeds and flowers, but it was quite common when SCCs fed on large tree nuts/seeds and flowers (e.g. *Platanus* seeds; *Magnolia* flowers). The increases in digging and the use of tree foraging substrates in winter probably reflected the greater reliance of urban SCCs in streetscapes on arboreal and sub-soil food resources in that season. Consumption of supplementary

food was very limited, unlike the situation in parts of central Sydney (Davis *et al.* 2017). However, we know that SCCs also consume supplementary food at garden feeders in Melbourne (Ruwandeniya and Lill 2016) and anecdotally that some individuals regularly do so at cafes (Fig. 6). Eating human food waste was also very limited.

Detailed published descriptions of nonurban SCCs' diet come mainly from mixed farming and cropland areas in north-eastern New South Wales (Noske 1980) and cropland in rural South Australia (Emison and Beardsell 1985) (Table 4). In the former area, cereal crop seeds (sunflower, sorghum *Sorghum*, wheat *Triticum*, oats *Avena* and barley *Hordeum*) from standing plants or stubble dominated the non-breeding season diet. Seeds and fruit of many native and exotic herbs, shrubs and trees formed a minor, but diverse, component of the diet at that time of year. Several of these plants also featured in the diet of SCCs in Melbourne (e.g. *Taraxacum*, *Arctotheca*, *Plantago* and *Romulea*). In nonurban South Australia, cereal crop grains also featured, although less prominently, in the SCC's winter diet, and Onion Grass corms were consumed in pasture land. These two components also featured prominently in the diet in nonurban Victoria (Emison and Nichols 1992), although the season when they were mostly consumed was unspecified. Supplementary food (cereal grains) is taken from spillages, feed trails and food storage facilities by nonurban SCCs (Noske 1980; Emison and Beardsell 1985).

Thus, the main dietary difference between urban and nonurban SCCs was the importance of cereal grains, a food source rarely present in cities, to some rural birds. Both populations consume seeds, roots and other components of a variety of herbs and trees, although native plants probably feature a little more prominently in nonurban environments than they did in Melbourne (Table 4).

Foraging behaviour

Noske (1980) describes nonurban SCCs feeding while walking on the ground, and digging with the beak for sown seed or corms (e.g. *Cymbonotus* sp.) i.e. ground-gleaning and digging like their Melbourne conspecifics. They also fed in

trees as urban individuals did, ‘chewing’ green, flowering or mature buds and consuming fruit of eucalypts and *Angophora*. Nonurban SCCs often hold larger food items in the foot during feeding, as described for urban conspecifics above. Three foraging behaviours observed in nonurban SCCs (Noske 1980) were not recorded for urban conspecifics in Melbourne in the non-breeding season: (a) perching on top of tall, sturdy monocots and consuming their seeds *in situ*, (b) cutting down or bending the stalk of less sturdy, tall monocots using beak and foot manipulation and then either consuming the seeds directly from the seed-head or detaching it and carrying it some distance before seed extraction and consumption, and (c) exploring livestock faeces for undigested seeds (Table 4).

Nonurban SCCs do not appear to have been observed using innovative foraging behaviours. We did not observe any use of truly innovative foraging behaviours in urban Melbourne either (Table 4). This is in striking contrast with what has been observed in Sydney recently (Jones 2019). Either: (a) we missed these innovative behaviours because of our observation strategy, (b) they occur primarily in the breeding season, when we made no observations, (c) they do not currently occur in Melbourne or (d) they only occur at very low frequencies. It is possible that SCCs exhibited such behaviour in the middle of the day and well away from their nocturnal roost, so that we would not have recorded it. However, although we focused mainly on observing foraging near roosts in the early morning and late afternoon, we did make some observations in the middle of the day. If innovative foraging behaviour was at all common it is unlikely that we would have completely missed it, but the possibility cannot be entirely excluded. It seems rather unlikely, although not impossible, that innovative foraging would be restricted to the breeding season. As innovative foraging on novel resources is learned and may well to some extent be culturally transmitted, conceivably it has either not yet arisen or not yet spread widely in Melbourne.

Interspecific association and agonistic interaction

Heterospecific birds were within 10 m of SCCs for well over half the time that the cockatoos were foraging. Seven species were involved, five of which were of a comparable size to SCCs and two much smaller (Table 3). However, only three (all close relatives of the SCC) of these seven species consume substantial volumes of one or more of urban SCCs’ main dietary items (namely the Little and Long-billed Corellas, and the Galah; Allen 1950; Noske 1980; Rowley 1990; Emison and Nicholls 1992; Emison *et al.* 1994; Lill and Polley 2020; Polley and Lill 2020). However, the Long-billed Corella was close to foraging SCCs on just 11% of the occasions when this variable was recorded, the Little Corella on just 6% and the Galah on <1%. Only Long-billed Corellas had a significant agonistic involvement with foraging SCCs; they interacted aggressively with them on 17% of the occasions when they were foraging nearby and spatially displaced them on over 90% of these occasions. This is interesting because, although the sample size was small, outcomes were quite consistent, which accords with the asymmetry that Martin *et al.*’s (2017) meta-analysis demonstrated. Displacement, however, was usually only for a few metres and the supplanted SCC(s) resumed foraging at the site very quickly. Thus, although heterospecifics commonly foraged close to foraging SCCs, agonistic behaviour between

them was infrequent and appeared to have a negligible effect on the cockatoos’ foraging efficiency. The significant costs often associated with aggressive interference competition (e.g. physical injury, reduced food intake; Ferry *et al.* 2016) seemed to be low for SCCs. Noske (1980) also found that aggressive interactions were rare in mixed flocks of SCCs and Galahs in non-urban NSW.

Our findings are consistent with those for several other recent urban colonizing bird species in Australia, including parrots, pigeons, mynas and ravens (Lowry and Lill 2007; Crisp and Lill 2008; Smith and Lill 2008, Stanford and Lill 2008; Lowe *et al.* 2011; Mulhall and Lill 2011; Lill and Hales 2015). There are, of course, some notable exceptions to this non-aggressive tendency among recent urban colonizers, such as Noisy Miners *Manorina melanocephala* (Lill and Muscat 2015). Nonetheless, these findings suggest that aggressive interference competition for food may not be a significant challenge for many of the recent avian colonisers of Australian cities, including SCCs. An influential factor in relation to the low level of interspecific aggression could be that the major food of SCCs in Melbourne was grass seeds and roots, a resource that is highly abundant in urban streets, parkland and sports fields, and which possibly may not be a limiting resource at current urban avian granivore population densities.

The observed low frequency of interspecific aggression between urban SCCs and closely related, co-habiting species with overlapping diets does not exclude the possibility of some food resource partitioning among them (Begon *et al.* 2006; Baker *et al.* 2014). However, this is unlikely to operate through cryptic interference competition (Gyimisi *et al.* 2010) resulting from learned avoidance by these related species driven by interspecific aggression exhibited by SCCs. Firstly, such an effect would presumably have to be reinforced trans-generationally and therefore one would expect to see a higher frequency of agonistic interaction between SCCs and closely related species than was evident in our study. Secondly, and more critically, SCCs only initiated the aggression in 23% of the observed interspecific agonistic interactions with closely related species. Such a low initiation rate is not what would be predicted if they were preventing close association with foraging members of related species through aggressive dominance. There is, however, likely to be interspecific competition for other resources; urban SCCs in Sydney aggressively defend natural nest hollows, which are a relatively scarce breeding resource, against other species (Davis *et al.* 2013, 2014).

Roosting behaviour

Roosting behaviour was not investigated quantitatively, but most of the small sample of 12 urban roosts recorded were in tall eucalypts quite close to water. In nonurban north-eastern New South Wales, SCCs roosted solely in eucalypts (Noske 1980) and in nonurban southern New South Wales they also roosted only in eucalypts in spring (Lindenmayer *et al.* 1996). Roosting in tall eucalypts may be common in both urban and nonurban environments and possibly another indication of preadaptation to the urban environment, although SCCs have been recorded roosting in *Casuarina*, *Melaleuca* and *Leptospermum* too in nonurban south-eastern Australia (Lamm and Calaby 1950; Cooper 1975). It is less clear whether proximity to water is a widespread feature of nonurban roosts.

Future research

These observations should be extended to encompass the breeding season because we expect that urban SCCs will consume additional foods and possibly exhibit additional foraging behaviours then. Conducting an online survey of ornithologists and bird observers to expand our knowledge of SCC use of supplementary food (and possibly human food waste) in Melbourne would also be valuable.

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