Corella, 2018, 42: 55-61

Doing what comes naturally: are Australian Wood Ducks *Chenonetta jubata* pre-adapted for feeding in cities?

Vincent Marsicovetere and Alan Lill

Department of Ecology, Environment and Evolution, School of Life Sciences, La Trobe University, Bundoora, Victoria 3083.
Email: A.Lill@latrobe.edu.au

Received: 27 January 2018
Accepted: 2 March 2018

Some birds are pre-adapted for urban feeding without needing to substantially exploit the abundant novel food sources occurring in cities. This is apparently so because many cities contain the same or similar food resources to those that these birds exploit in nonurban environments, which they can therefore exploit in familiar ways, and for access to which they experience little interspecific competition. Endemic Wood Ducks *Chenonetta jubata* are common in many eastern Australian cities. We determined whether they conform to this pre-adaptation syndrome by documenting: (1) their diet, foraging behaviour and involvement in interspecific interference competition for food in urban Melbourne, Australia and (2) their foraging habitat use in urban Melbourne and nearby nonurban areas. Australian Wood Ducks' urban diet predominantly comprised grass leaves (72%) acquired by grazing (78% of foraging behaviour); supplementary food (bread) provided by humans was the focus of only 2% of their feeding. This pattern conforms with several published descriptions based on nonurban observations. Habitat immediately around foraging Wood Ducks was similar in urban and nonurban environments, particularly with respect to the area of short grass and herbs suitable for foraging, the area of free-standing water, and the percentage tree canopy cover. The species most commonly foraging close to Wood Ducks were the Eurasian Coot *Fulica atra* and Pacific Black Duck *Anas superciliosa*, for both of which grass is a minor, but significant, dietary constituent in cities. However, neither these species nor foraging neighbours of seven other bird species were involved in significant interference competition with foraging Wood Ducks. Thus, Wood Ducks seem to be pre-adapted for foraging in urban Melbourne (and probably other cities) because the city contains an abundant, familiar food resource that can be exploited using a familiar behaviour, apparently with little interference competition from other resident bird species.

INTRODUCTION

Food abundance is greater in urban than nonurban environments for many birds that exploit the large volume of human food waste available in cities (Sol 2008; Newsome and van Feden 2017; Macías-Garcia *et al*. 2017). The ability to adjust foraging behaviour, often innovatively, to exploit this novel food source is a key factor facilitating urban colonization by many bird species (Sol *et al*. 2011), notwithstanding some negative effects that can be associated with such exploitation (Jones 2011; Murray *et al*. 2016). This adjustment may involve behavioural plasticity and/or pre- or post-colonization microevolutionary changes (Miranda 2017). The result is often urban populations comprising individuals that exploit both natural and novel food resources substantially – what Blair (1996) termed 'urban adapters'.

However, we often overlook the fact that in some cases successful urban colonization does not apparently involve either much behavioural flexibility or microevolutionary change. A subset of urban colonizer species appears to be inherently suited (or pre-adapted, McDonnell and Hahs 2015) for feeding in cities without substantially exploiting novel food sources. This happens when the urban environment, although highly modified in many respects, nonetheless contains abundant food resources that are familiar to these colonizers in their nonurban range and which they can exploit using familiar behaviours (Lowry and Lill 2007; McDonnell and Hahs 2015).

Even when such circumstances occur, however, access to the familiar food resources by a potential colonist species could theoretically be limited by competition (involving aggressive interference and/or competitive exclusion), with members of long-established, resident urban species with a similar feeding ecology (Shochat *et al*. 2006; Møller *et al*. 2012). Alternatively, if such competition is negligible or can be dominated by the 'newcomer' species, the combination of familiar food resources accessible by familiar behaviours without effective interspecific competition could greatly facilitate urban colonisation.

Endemic Australian Wood Ducks *Chenonetta jubata* (41-55 cm) are widespread in grasslands, open woodlands, wetlands, farmland and coastal inlets (Menkhorst *et al*. 2017). They have increased in abundance and distribution since the mid-20th century (Briggs *et al*. 1985) and are now quite common in many cities. Descriptions of their foraging based on nonurban observations categorize them as being predominantly terrestrial grazers on short grass, clover and other herbs, although they also consume grain, and insects caught on land and by freshwater dabbling (Lavery 1971; Frith 1982; Kingsford 1986, 1989; Marchant and Higgins 1990). Mowed, short grass and herbs are abundant in urban gardens, parks and sporting facilities (Silva *et al.* 2015), so urban Wood Ducks may conceivably not need to supplement their diet significantly through feeding (innovatively or otherwise) on novel foods deliberately or unintentionally provided by humans, although some other native Australian dabbling ducks do so e.g. Pacific Black Duck *Anas superciliosa* (Chapman and Jones 2009, 2012).

With respect to its feeding, the Wood Duck *may* thus potentially not be truly an 'urban adapter', substantially exploiting both natural and anthropogenic food resources in cities (Blair 1996), but rather a species pre-adapted for feeding in the urban environment that exploits mostly natural rather than anthropogenic food resources there (McDonnell and Hahs 2015). A lack of effective interspecific competition for these food resources would further facilitate urban settlement by Wood Ducks.

Our aims here were to: (1) document adult Wood Ducks' diet and foraging behaviour in Melbourne – to determine the relative extent to which urban Wood Ducks exploit familiar and novel food resources, (2) determine how similar foraging habitat use by Wood Ducks is in Melbourne and nearby nonurban areas – to assess whether urban colonization has involved changes in foraging habitat use, and (3) document which bird species adult urban Wood Ducks tolerate/do not tolerate foraging close to them – to elucidate the extent to which interspecific competition may influence Wood Ducks' urban foraging ecology.

METHODS

Study area

The investigation was conducted from April to August (austral autumn and winter), 2017 in urban Melbourne (37º50' S 145º00 E), Australia and nearby nonurban areas up to ~100 km from the city's CBD. The latter part of this period overlapped the Wood Duck's breeding season in this region (July to December). Melbourne (population >5 million people, area > 9,000 km^2) has numerous natural and artificial freshwater bodies which, with their immediately surrounding parkland and wetland habitat, provide a suitable environment for many water birds. During the investigation, monthly mean maximum and minimum ambient temperatures in Melbourne varied from 6.7 to 10.8º C and 15.0 to 20.3º C, respectively, and monthly precipitation from 43 to 53 mm.

Foraging behaviour and diet

Adult Wood Ducks' foraging behaviour was recorded at 12 locations widely spread throughout urban Melbourne, which were found by: (a) inspecting *Google Earth* satellite images for likely locations, and (b) systematically exploring suburbs by vehicle. Some locations were used more than once, but a 42-day 'minimum return time' for the observers increased independence of data obtained from such sites.

Foraging behaviours were:

a. Terrestrial – [i] grazing (cropping pieces of vegetation from a plant with the beak), and [ii] gleaning (picking food items off a substrate with the beak).

b. Aquatic – [i] beak-dipping (beak dipped in top cm or so of water column to clasp food item), and [ii] head-dipping (head, and sometimes neck, immersed several cm below water surface to clasp food item in beak, occasionally with upending). These latter two dabbling behaviours were used to procure aquatic vegetation and insects.

Focal individuals foraged solitarily or, more commonly, in quite compact flocks of varying size. The observer stood ≥10 m from the focal duck and there were usually few other people nearby. In flocks of 2-3 ducks, only one focal individual was observed, always the individual furthest to the left from the observer's viewpoint. In flocks ≥ 4 ducks, two focal individuals were observed, the second bird always arbitrarily being the bird farthest to the observer's right. As members of a flock typically foraged in a similar manner, especially on land, we did not systematically examine whether flock size influenced foraging behaviour. One foraging event elapsed before recording on a focal duck commenced, and up to three events were recorded per focal individual per observation session. A foraging event was defined as behaviour resulting in a Wood Duck acquiring and consuming food. This could be a single item taken in a single peck if the focal bird was gleaning or beak-dipping, or several pieces of vegetation taken in several rapid pecks between successive brief pauses in grazing. It was impossible to accurately quantify grazing in terms of single pecks, as the behaviour proceeded too rapidly. Once the observer had obtained up to three records for one or two (in flocks ≥ 4 ducks) focal individuals, he moved at least 10 m and often much further away from the focal bird(s) before selecting another individual to observe. Focal birds' sex was determined from their obvious plumage differences (Figure 1).

Figure 1. *Australian Wood Ducks in a short grass foraging area near water in urban Melbourne parkland. Male nearest and female furthest from the camera.*

The substrate supporting the focal foraging adult Wood Duck was recorded as: grass, bark mulch, solid surface (rock, cement, bitumen etc.), water or 'other'. Where possible, the food item's identity was recorded, but many items (especially aquatic ones) could not be identified. Specimens of some of the grass species consumed were collected, preserved and identified to genus with the help of published identification guides and expert knowledge.

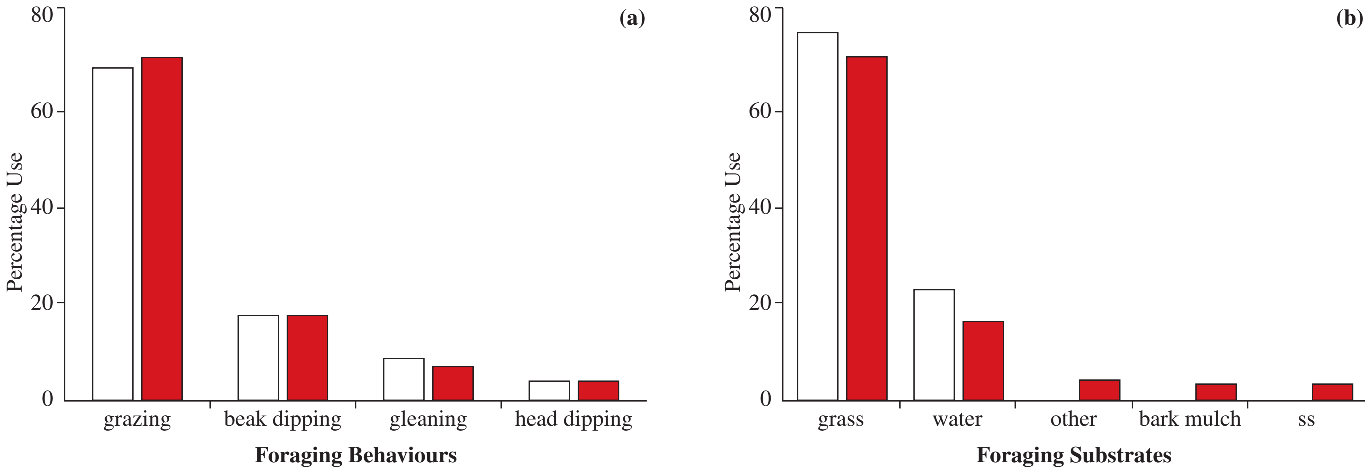

Figure 2. *Percentage use of (a) foraging behaviours and (b) substrates by adult female (white bars; n = 117) and male (red bars; n = 91) urban Australian Wood Ducks based on all records for focal birds. Percentages are of the total number records obtained during the investigation. Note that bars collectively do not always total exactly100% due to rounding. ss = solid surface (e.g. rock, bitumen). There was no difference between the distributions for males and females of behaviours* $\chi 2(3) = 0.532$, $p = 0.912$, *but there was a difference for substrates* $\chi 2(2) = 8.745$, $p = 0.013$ *(some necessary category pooling).*

Heterospecific neighbours and agonistic interactions

While recording adult Wood Ducks' foraging in urban Melbourne, the number and species identity of all heterospecific birds within a visualized 10 m of the focal Wood Duck were noted, except when there was more than one focal individual in a Wood Duck flock and the same neighbours would have been recorded for more than one focal individual.

Agonistic interactions between a focal, foraging adult Wood Duck and heterospecific birds were systematically recorded, foraging observations being momentarily suspended to facilitate this recording. Variables recorded were: (1) the species involved, (2) the nature of the interaction (threat, attack or pursuit), and (3) the outcome (one combatant retreated < 10 m, usually on foot; one combatant flew away ≥10 m).

Foraging habitat 'snapshots'

Diurnal foraging habitat use of urban and nonurban Wood Ducks was compared by taking habitat 'snapshots' around the locations of sightings of foraging Wood Ducks. Urban 'snapshots' came mainly from widely spread areas of Melbourne up to 41 km from the CBD, but were supplemented by three 'snapshots' from built environment in two regional Victorian towns (Gisborne 37.4900º S, 144.5889º E and Riddell's Creek 37.4438º S, 144.6832º E). Nonurban 'snapshots' came from widely dispersed rural sites up to 104 km from Melbourne's CBD in all main compass directions. There was a bias towards sites near roads because of the necessity of finding sites by searching from a vehicle.

The exact location of a Wood Duck sighting was temporarily recorded on a *Google Earth* satellite image or map on a cell phone and later transposed onto a larger *Google Earth* satellite image on a personal computer. Using the Polygon Tool in *Google Earth* (*Ruler* window in *Tools* menu), a 100 m^2 square was drawn on the image on the screen, with the Wood Duck sighting located centrally in it; all such squares had a similar orientation. The areas (ha) of the square occupied by potentially suitable foraging habitat (short grass and herbs), tree canopy, freshwater bodies and built environment were then outlined with the tool and their areas automatically measured. Additionally, linear distances (± 1 m) of the sighted Wood Duck(s) from the nearest freshwater body and nearest substantial (at least 1 km^2) block of built environment were measured on the screen images with the Line tool in *Google Earth* (*Ruler* window in *Tools* menu).

Data analysis

Variation in Wood Ducks' foraging behaviour and substrate use was so limited that sophisticated statistical modelling was unnecessary. Possible sex differences in foraging were analyzed with r × k chi squared tests of independence. Components of urban and nonurban habitat 'snapshots' were compared with independent, two-tailed *t*-tests after log or logit data transformation to increase conformity with the test's assumptions of normality and homoscedasticity (Quinn and Keough 2002). Although multiple *t*-tests were used in this analysis, the comparisons were between two distinct environments and the variables were also mostly independent within a sampled snapshot.

RESULTS

Foraging behaviour and diet

Adult Wood Duck foraging records (n = 210, from 68 focal individuals) were obtained throughout the period April to August 2017 in parkland (95% of records) and wetlands dispersed widely throughout urban Melbourne. There was no disparity between the foraging behaviour profiles of adult males and females (Figure 2a). The sexes used foraging substrates differently, but only in that males utilized the minor foraging substrates (bark mulch, solid surfaces and 'other') collectively more than did females; males, like females, still predominantly used grass and water for foraging (Figure 2b). For both the foraging behaviours and the substrates used, there was essentially no difference between the distributions derived from first and all records obtained from focal birds (Figure 3a, b), to the extent that statistical verification was superfluous.

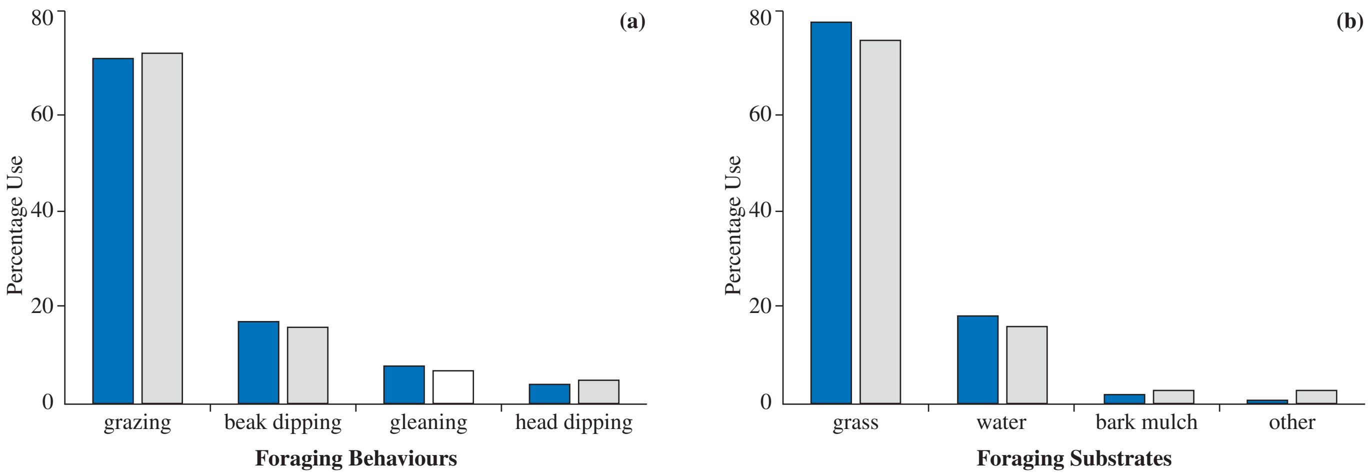

Figure 3. *Percentage use of foraging (a) behaviours and (b) substrates by urban Australian Wood Ducks based on all records (blue bars, n = 210) and first records (pale grey bars; n = 73) for focal birds. Percentages are of the total number records obtained during the investigation. Note that bars do not always collectively total exactly 100% due to rounding.*

Table 1

Comparison of urban and nonurban foraging habitat 'snapshots' for adult Australian Wood Ducks. Degrees of freedom = 82, except for area of closest water body to ducks (df. = 81). Significant differences (alpha = 0.05) shown in bold font. Areas in ha and linear distances in m.

Variable	Mean (± SE.) urban	Mean (±SE.) nonurban	*t*-value	p-value
Estimated terrestrial foraging area	0.79 (0.03)	0.85 (0.03)	1.074	0.286
Total tree canopy area	0.19 (0.03)	0.16 (0.02)	1.27	0.208
Area of water	0.19 (0.03)	0.10 (0.03)	1.894	0.062
Area of water body closest to sighted ducks	**9.52 (6.73)**	**0.24 (0.06)**	**4.131**	**<0.001**
Area of built environment	0.03 (0.01)	0.02 (0.01)	0.987	0.327
Distance of sighted ducks from water	**326.5 (90.6)**	**110.8 (43.6)**	**3.769**	**<0.001**
Distance to nearest built environment	**235.4 (43.4)**	**9947 (3429.5)**	**12.361**	**<0.001**

Based on all records for both sexes combined, the frequencies at which urban adult Wood Ducks performed the four types of foraging behaviour observed varied 18-fold; grazing (71% of records) was the dominant foraging behaviour, with aquatic beak-dipping (17%) the second most common pattern (Figure 3a, blue columns). The frequencies at which foraging occurred on the five substrates used varied 78-fold; predictably, grass (78% of records) was the most common and water (18%) the second most common substrate utilized (Figure 3b, blue columns).

The diet of urban adult Wood Ducks (*n* = 212 feeding records) comprised mainly grasses (72%), including species in the genera *Poa, Pennisetum* and *Cynodon*, although many could not be identified. Wood-sorrels *Oxalis* sp. were also consumed. Unidentified items taken from the water comprised a further 22% of the diet. Feeding on novel foods was limited, being restricted to the very occasional consumption of bread intentionally provided by humans (2%).

Foraging habitat

On average, there was no difference in the 1 ha habitat 'snapshots' around diurnal foraging locations of Wood Ducks in urban (n = 37) and nonurban (n = 47) environments with respect to: (1) the estimated area suitable for foraging (means: 79% urban and 85% nonurban environment), (2) percentage tree canopy cover, or (3) areas of free-standing water and built environment (Table 1). However, on average, urban individuals foraged 3× further away from open water, their nearest water body was 40× larger and they were 42× closer to a substantial block of built environment than were nonurban conspecifics (Table 1).

Foraging neighbours and agonistic interactions

Forty-three percent of foraging adult urban Wood Ducks had one or more heterospecific birds within an estimated 10 m of them. Nine species were involved, six being water birds. The most common neighbours in terms of both presence and absolute numbers were Pacific Black Ducks and Eurasian Coots *Fulica atra* (Table 2). However, only five interspecific agonistic interactions involving urban adult Wood Ducks were observed, a very low rate of 0.023 interactions per foraging record or 0.074 per focal foraging Wood Duck. Three species were involved, Pacific Black Duck and Eurasian Coot (2 interactions each) and Purple Swamphen *Porphyrio porphyrio.* One interaction each with a Eurasian Coot, a Purple Swamphen and a Pacific Black Duck resulted in the Wood Duck involved moving away, but < 10 m. The other two interactions both resulted in the heterospecific participant (a Black Duck and a Eurasian Coot, respectively) flying > 10 m away.

Table 2

Occurrence of heterospecific birds close to foraging adult urban Australian Wood Ducks.

Species	Number of instances	Total number of individuals
Eurasian Coot *Fulica atra*	9	112
Pacific Black Duck *Anas superciliosa*	9	66
Purple Swamphen *Porphyrio porphyrio*	3	5
Silver Gull *Chroicocephalus novaehollandiae*	2	9
Dusky Moorhen *Gallinula tenebrosa*	2	7
Chestnut Teal *A. castanea*	1	9
Domestic Duck *A. platyrhynchos domesticus*	1	1
Australian White Ibis *Threskiornis molucca*	1	56
Sulphur-crested Cockatoo *Cacatua galerita*	1	12
TOTAL	**29**	**277**

DISCUSSION

Foraging behaviour and habitat

Adult urban Wood Ducks foraged solitarily or in flocks of various sizes. They predominantly fed by grazing on grass leaves in areas of short grass and herbs in parkland and wetlands. Note that the method necessarily used to score grazing (several rapid pecks per grazing event) if anything probably underestimated the predominance of grazing. Wood Ducks also fed on freshwater bodies by beak- and head-dipping (dabbling), but to a much lesser extent. Notably, foraging on food intentionally or unintentionally supplied by humans was rare and the behaviour involved was not novel, being essentially gleaning. Chapman and Jones (2009) also found that although Wood Ducks comprised 21% of the duck population in parks in urban Brisbane (27.4698° S, 153.0251° E), they accounted for only about 6% of the ducks being fed by park visitors. In contrast, Pacific Black Ducks comprised 74% of the ducks consuming bread provided by the Brisbane public, although this consumption did not greatly affect their foraging on natural food sources (Chapman and Jones 2011). More generally, ducks may be poorly equipped to consume human food waste in highly manipulative ways because of their bill morphology and webbed feet.

The foraging profile and diet of Wood Ducks in urban Melbourne accorded well with descriptions of the species' feeding derived from several nonurban populations (summarised in Marchant and Higgins 1990). Frith (1957, 1959) found that ~ 58% of Wood Ducks' largely vegetarian diet near rural rice farms in New South Wales (NSW) comprised land plants, with the leaves of various grass and sedge species being dominant. Kingsford (1986, 1989) demonstrated that in a rural agricultural landscape in NSW during the breeding season, 99% of Wood Ducks' diet comprised terrestrial plant material; grazing (which occupied 33% of daytime) comprised 95% and gleaning insects from the water 5% of their feeding behaviour. Urban Pacific Black Ducks also forage on natural resources in a similar manner to that which they employ in nonurban areas. However, in contrast with urban Wood Ducks, they also consume a lot of food provided by humans and use novel feeding behaviours in so doing (Chapman and Jones 2012) i.e. with respect to food resources, they are 'urban adapters' *sensu* Blair (1996).

Habitat 'snapshots' of the local areas in which Wood Ducks foraged diurnally were very similar for urban and nonurban locations, particularly with respect to the high percentage of short grass and herb areas suitable for foraging (grand mean 82%). The only differences were that urban Wood Ducks foraged further away from water than nonurban conspecifics, their nearest water body was typically larger and, not surprisingly, they fed much closer to substantial areas of built environment. The first two disparities reflect the fact that nonurban Wood Ducks occurred mainly adjacent to, or on, the small dams which most rural Victorian properties have for water storage. In rural south-western Australia (Saunders 1993) and NSW there is a similar association of Wood Ducks with farm dams, which provide water in which the ducks can bathe, drink, mate and especially escape predators. These dams are usually adjacent to pasture suitable for grazing, and Wood Ducks rarely ventured >100 m from a dam when feeding in rural NSW (Kingsford 1992). Such dams are less common in large cities where properties mostly have a mains water supply. Many water bodies in Melbourne parkland are recreational or ornamental ponds and lakes rather than water storages, and are much larger than the typical rural Victorian farm dam.

We acknowledge that we did not directly compare Wood Ducks' foraging behaviour in urban Melbourne and nonurban Victoria, but in view of the published descriptions of Wood Ducks' foraging in several nonurban areas (Lavery 1971; Frith 1957, 1959; Kingsford 1989) it seems virtually certain that it is very similar. The large areas of regularly mown grass in Melbourne parks, sports fields etc. provide an abundant, generally familiar food resource for Wood Ducks that they can exploit in a familiar way by grazing. Of course, the habitat 'snapshots' are just that; a more extensive and detailed documentation of Wood Ducks' foraging habitat use is desirable to check whether our conclusion about the similarity of urban and nonurban foraging habitat drawn from the snapshots is supported. It would also be valuable to determine the extent to which the same plant species are consumed in the two environments, because Kingsford (1986) found that in addition to Poaceae species, species of Leguminosae featured prominently in Wood Ducks' diet in rural NSW pastureland. Casual observation (Lill, unpublished data) suggests that Wood Ducks in Melbourne feed similarly in spring and summer to the way in which we observed them feeding in autumn and winter, but this needs to be checked rigorously.

Interspecific competition

The presence of familiar resources may be insufficient to permit urban colonization if there are already resident species with a similar ecology to that of the potential colonist that are likely to compete successfully for those resources. However, such competition could be dominated through aggressive behaviour or reduced through competitive exclusion (Duncan *et al.* 2003). If interference competition for food is operative, we might expect the species involved to quite commonly feed close together, but frequently interact aggressively; if niche partitioning is occurring, we would not often expect to see members of the potentially competing species foraging in a similar manner close together.

Just over forty percent of foraging urban adult Wood Ducks had heterospecific birds foraging close to them. Nine species were involved, but of these only the Eurasian Coot and Dusky Moorhen *Gallinula tenebrosa* feed significantly on grass (Marchant and Higgins 1990). Coots were present on 31% and Dusky Moorhens on just 7% of the occasions when focal foraging urban Wood Ducks had one or more close heterospecific neighbours. However, only two Wood Duck × Eurasian Coot agonistic interactions were observed (one dominated by the coot and the other by the duck), and no Wood Duck × Dusky Moorhen interactions were seen. Overall, the frequency of agonistic interactions between foraging Wood Ducks and heterospecific birds was extremely low.

There was thus no compelling evidence of significant aggressive interference competition between Wood Ducks and other resident urban bird species that have a terrestrially-acquired diet component that is also consumed by Wood Ducks. Setting aside interactions at artificial feeders, a comparable conclusion has been reached for several other recent urban colonist bird species in Melbourne, including some lorikeets, parrots, pigeons, ravens and mynas (e.g. Crisp and Lill 2006; Lowry and Lill 2007; Stanford and Lill 2008; Mulhall and Lill 2011; Lill and Hales 2015), although highly aggressive Noisy Miners *Manorhina melanocephala* are notable exceptions (Lill and Muscat 2015). Aggressive competition for food would not appear to present an obstacle to settlement of established cities by Wood Ducks and many other Australian native birds if this widespread post-colonization lack of interspecific interference competition reflects the situation at the inception of urban colonization. Whether this is so is unknown, but perhaps we might expect an urban colonist bird species to encounter a relatively low level of interspecific competition for resources at the establishment phase of colonization because of the low diversity of resident bird species that is characteristic of cities, and hence the relatively low biotic resistance that colonizers are likely to encounter (Shea and Chesson 2002).

A second reason why there might be a low frequency of interference competition for food could be that the food resources in question are superabundant in cities (Newsome and van Feden 2017). For example, turf grass covers ~2% of continental USA, much of it being in towns and cities which collectively occupy 3.5-5% of the country's landmass (Milesi *et al.* 2005). It is also very abundant in Australian cities; many grass species in the genera *Poa* and *Cynodon*, which featured in urban Wood Ducks' diet, have the growth and colonising properties of weeds and are widespread in Australian conurbations. There also appear to be very few bird species in Melbourne, other than Wood Ducks, whose main food is grass and herb leaves, although possible niche partitioning between Wood Ducks and those species that consume some grass (*e.g.* Dusky Moorhens and Black Swans *Cygnus atratus*; Frith *et al.* 1969) warrants further examination. There could also potentially be some dietary overlap and niche partitioning with other co-habiting dabbling ducks, particularly Pacific Black Ducks, with respect to waterborne food items. However, dabbling comprised only ~ 21% of Wood Ducks' urban foraging, so divergence with respect to this component of the diet may not be critical.

There could be competition between Wood Ducks and heterospecifics for other critical resources, particularly nest sites. Wood Ducks use secondary tree cavities for nesting (Marchant and Higgins 1990). This resource is exploited by many other birds and mammals in southern Australia (Gibbons and Lindenmayer 2002), appears to be limiting and is a source of interspecific competition in cities (Davis *et al.* 2013). This would be an interesting focus for further research.

CONCLUSIONS

The Australian Wood Duck appears to be pre-adapted for foraging in urban Melbourne and probably other Australian conurbations because city parks, gardens and sports fields contain abundant short grass and herbs; this is a familiar food resource, that can be exploited by grazing, a familiar behaviour, without significant interference competition with other resident bird species. Thus, with respect to its food resources at least, the Wood Duck is not really an 'urban adapter', but rather a non-adapter that relies largely on natural food resources in cities. Adjustments in foraging behaviour through phenotypic plasticity or pre- or post-colonization microevolution appear to have been unnecessary to facilitate urban feeding by Wood Ducks – they just do what comes naturally! Nonetheless, it is unlikely that the Wood Duck is a species whose natural habitat has simply been taken over by urbanization i.e. that it is not truly an urban colonizer (Miranda 2017). Urban settlement by Wood Ducks seems to be recent, and the short grass habitat that they exploit for feeding in cities is a deliberate product of the urbanization process rather than a remnant that has merely survived the process. It is quite likely, of course, that Wood Ducks have had to actively adjust to some of the other challenges posed by urban life, such as high levels of human disturbance, noise and light pollution, and predation by cats (Lowry *et. al.* 2013; Macias Garcia *et al.* 2017).

Given the abundance of short grasses and herbs in urban parklands, sports fields and gardens, it is pertinent to ask whether being pre-adapted for urban feeding is widespread among grazing birds? Although they use other food resources and behaviours, grazing on grass leaves features prominently in the foraging of Canada Geese *Branta canadensis.* However, although individuals overwintering in urban Chicago, USA used 'green space' more than expected relative to its occurrence, they also showed marked behavioural flexibility and innovation in their urban habitat use and diet selection (Dorak *et al.* 2017). Thus, the pre-adaptation syndrome is clearly not a complete explanation for successful urban foraging in some grass grazing birds. More broadly, it would also be interesting to consider the extent to which the syndrome is applicable to some grass grazing urban mammals, for example Elk *Cervus canadensis* that feed in some North American cities.

ACKNOWLEDGEMENTS

We thank Simon Watson for statistical guidance, John Morgan for helping to identify grasses, Sally Bowen for helping with data collection and Darryl Jones for helpful comments on the manuscript. The study conformed to all ethical standards required for conducting research on free-living vertebrates in Victoria, Australia.

REFERENCES

Blair, R.B. (1996). Land use and avian species diversity along an urban gradient. *Ecological Applications* **6**: 506–519.

Briggs, S.V., Maher, M.T. and Palmer, R.P. (1985). Hunter activity and waterfowl harvests in New South Wales, 1977-82. *Australian Wildlife Research* **12**: 515-522.

Chapman, R. and Jones, D. J. (2009). Just feeding the ducks: quantifying a common wildlife-human interaction. *Sunbird* **39:** 19-28.

Chapman, R. and Jones, D. (2011). Foraging by native and domestic ducks in urban lakes: behavioural implications of all that bread. *Corella* **35**: 101-106.

Chapman, R. and Jones, D. (2012). Synurbanisation of Pacific Black Ducks *Anas superciliosa* in south-eastern Queensland: the influence of supplementary feeding on foraging behaviour. *Australian Field Ornithology* **29**: 31-39.

Crisp, H. and Lill, A. (2006). City slickers: habitat use and foraging in urban Common Mynas *Acridotheres tristis*. *Corella* **30**: 9-15.

Davis, A., Major, R. E. and Taylor, C. E. (2013). Housing shortages in urban regions: aggressive interactions at tree hollows in forest remnants. *PlosOne* **8**(3): e59332.

Dorak, B.E., Ward, M.P., Eichholz, M.W., Washburn, B.E., Lyons, T.P. and Hagy, H.M. (2017). Survival and habitat selection of Canada Geese during autumn and winter in metropolitan Chicago, USA. *Condor Ornithological Applications* **119**: 787-799.

Frith, H.J. (1957). Wild ducks and the rice industry in New South Wales. *CSIRO Wildlife Research* **2**: 32-50.

Frith, H.J. (1959). The ecology of wild ducks in inland New South Wales III. Food habits. *CSIRO Wildlife Research* **4**: 131-155.

Frith, H. J., Braithwaite, L.W. and McKean, J. L. (1969). Waterfowl in an inland swamp in New South Wales. 2. Food. *CSIRO Wildlife Research* **14**: 17-64.

Gibbons, P. and Lindenmayer, D. (2003). *Tree hollows and wildlife conservation in Australia*. CSIRO Publishing, Collingwood, Victoria.

Jones, D. (2011). An appetite for connection: why we need to understand the effect and value of feeding wild birds. *Emu* **111**: i-vii.

Kingsford, R.T. (1986). Reproductive biology and habitat use by the Maned Duck *Chenonetta jubata* (Latham). PhD. thesis, University of Sydney.

Kingsford, R. T. (1989). Food of the Maned Duck *Chenonetta jubata* during the breeding season. *Emu* **89**: 119-124.

Kingsford, R.T. (1992). Maned ducks and farm dams: a success story. *Emu* **92**: 163-169.

Lavery, H.J. (1971). Studies of waterfowl in North Queensland 6. Feeding methods and foods. *Queensland Journal of Agricultural and Animal Sciences* **28**: 255-273.

Lill, A. and Hales, E. (2015). Behavioural and ecological keys to urban colonization by Little Ravens *(Corvus mellori)*. *Open Ornithological Journal* **8**: 22-31.

Lill, A. and Muscat, I. (2015). Importance of inherent suitability, behavioural flexibility and competitiveness in occupancy of urban parks by an endemic honeyeater. *Avian Biology Research* **8**: 227-236.

Lowry, H. and Lill, A. (2007). Ecological factors facilitating city-dwelling by red-rumped parrots. *Wildlife Research* **34**: 624-631.

Lowry H., Lill, A. and Wong, B. B.M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews of the Cambridge Philosophical Society* **88**: 537–549.

Macías-Garcia, C., Suarez-Rodriguez, M. and Lopez-Rull, I. (2017). Becoming citizens: avian adaptations to urban life. In: E. Murgui and M. Hedblom (eds.) *Ecology and conservation of birds in urban environments*. Springer International Publishing.

Marchant, S. and Higgins, P.J. (eds.) (1990). *Handbook of Australian, New Zealand and Antarctic Birds. Vol 1. Ratites to ducks*. Oxford University Press, Melbourne.

McDonnell, M. J. and Hahs, A. K. (2015). Adaptation and adaptedness of organisms to urban environments. *Annual Review of Ecology, Evolution and Systematics* **46**: 261–80.

Menkhorst, P. Rogers, D., Clarke, R., Davies, J., Marsack, P. and Franklin, K. (2017). *The Australian Bird Guide*. CSIRO Publishing, Clayton, Australia.

Milesi, C., Running, S. W., Elvidge, C. D., Dietz, J. B., Tuttle, B. J. and Nemani, R. R. (2005). Mapping and modeling the biogeochemical cycling of turf grasses in the United States. *Ecological Management* **36**: 426-438.

Miranda, A. C. (2017). Mechanisms of behavioural change in urban animals: the role of microevolution and phenotypic plasticity. In: E. Murgui and M. Hedblom (eds.) *Ecology and conservation of birds in urban environments.* Pp. 113-134. Springer International Publishing.

Møller, A. P., Diaz, M., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Markó, G. and Tryjanowski, P. (2012). High urban population densities of birds reflect their timing of urbanization. *Oecologia* **170**: 867-875.

Mulhall, S. and Lill, A. (2011). What facilitates urban colonization by crested pigeons *Ochyphaps lophotes*? *Corella* **35**: 73-81.

Murray, M. H., Becker, D. J., Hall, R. J. and Hernandez, S. M. (2016). Wildlife health and supplemental feeding: A review and management recommendations. *Biological Conservation* **204 B**: 163-174.

Newsome, T. M. and van Feden, L. M. (2017) The effects of food waste on wildlife and humans. *Sustainability* **9**: 1269.

Quinn, G. P. and Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.

Saunders, D.A. (1993). A community-based observer scheme to assess avian responses to habitat reduction and fragmentation in south-western Australia. *Biological Conservation* **64**: 203-218.

Shea, K. and Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* **17**: 170–176.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E. and Hope, D. (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution* **21**: 661-662.

Sol, D. (2008). Artificial selection, naturalization, and fitness: Darwin's pigeons revisited. *Biological Journal of the Linnaean Soc*iety **93**: 657–665.

Sol, D., Griffith, A. S., Bartomeus, I. and Boyce, H. (2011). Exploring or avoiding novel food sources? The novelty conflict in an invasive bird. *PlosONE* **6**(5): e19535.

Sol, D., Gonzalez-Lagos, C., Lapiedra, O. and Dıaz, M. (2017). Why are exotic birds so successful in urbanized environments? In: E. Murgui and M. Hedblom (eds.) *Ecology and conservation of birds in urban environments.* Pp. 75-90. Springer International Publishing.

Silva, C. P., Garcia, C. E., Estay, S. A. and Barbosa, O. (2015). Bird richness and abundance in response to urban form in a Latin American city: Valdivia, Chile as a case study. *PlosONE* **10**(9): e0138120.

Stanford, L. and Lill, A. (2008). Out on the town: feeding ecology of lorikeets in urban parkland. *Corella* **32:** 49-57.