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Reproductive effort of urban Little Ravens: nest site selection and brood defence

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Altricial birds' reproductive effort typically includes choosing an optimal nest site and protecting it in some manner against species constituting a threat to successful breeding. Pairs of urban Little Ravens *Corvus* mellori nested predominantly in tall eucalypts with a broader, denser canopy and fewer neighbouring trees of similar or greater height than control trees 100 m distant. Nest-trees also had fewer neighbouring trees of similar or greater height and 1.2 x greater estimated visibility over 100 m horizontally at nest height than nearby paired control trees of the same height. The main advantage of such distinctive nest sites may be providing superior surveillance for intruding nest predators and competing conspecifics. Nine identified bird species invaded Little Raven nest-trees during breeding, particularly honeyeaters and lorikeets; twenty-seven bird species intruded into 40 m zones around Little Raven nest-trees, the most frequent being the types of bird mentioned above and Common Mynas *Acridotheres tristis*. However, Little Ravens defended their nest site aggressively, and usually successfully, only against potential nest predators (currawongs and magpies) and competing conspecifics. Aggressive response rates to intrusions by these species, however, appeared to be rather low, but many possible factors affecting brood defence decisions were unknown in this study and may be influential. Literature indicates that the main species eliciting brood defence in other *Corvus* species are (1) raptors, including predators and nest usurpers of corvids, (2) other known predators of avian broods (e.g. kookaburras), (3) large (e.g. cockatoos) and smaller (e.g. pigeons and honeyeaters) birds seemingly posing little threat to nesting corvids, and (4) competing conspecifics. Reproductive effort expended on nest site selection by urban Little Ravens was probably limited, given the frequent re-use of nests. However, aggressive brood defence appeared costly, mainly because of the energetic behaviour and likely injury risk involved rather than the actual response rate.

INTRODUCTION

Reproductive effort (RE) is the percentage of an organism's current energy budget devoted to reproductive success. Life history theory predicts a trade-off between current and future reproduction; it is hypothesised that elevating RE increases current reproductive success, but decreases survivorship and/or future fecundity (Roff 1992). The trade-off is predicted as a large RE is usually costly because it is likely to require diversion of energy from growth and maintenance, and consequently impairment of other vital functions (e.g. immune competence; Hanssen *et al*. 2005). In altricial birds, RE is expended *inter alia* on parental care, including choosing an optimal nest site and protecting the nest, clutch and brood against species posing a threat to breeding success (hereinafter 'brood defence').

Nest sites' physical characteristics influence avian breeding success in several ways and choosing an optimal site is therefore critical and may require substantial time and energy allocations. Nest predation is a major cause of avian breeding failure, so in vulnerable species natural selection should favour individuals that choose nest sites with a low predation risk because of their inconspicuousness or inaccessibility (Fontaine and Martin 2006; Remes *et al*. 2012; LaManna *et al*. 2015). Both properties can also be important in reducing the risk of fitness losses through brood parasitism (Fiorini *et al*. 2009). Sheltered nest sites can be beneficial thermally through reducing heat loss by incubating and brooding parents, decreasing egg warming costs after nest recesses, and increasing nestlings' growth rate (Martin *et al*. 2017). Sites with low ectoparasite densities are likely to have lower nestling mortality attributable to blood-borne pathogens (Loye and Carroll 1998).

Another line of resistance against nest usurpation, nest predation, brood parasitism and extra-pair copulations is aggressive interception of intruders posing such threats. However, because this strategy is inherently costly and risky, there is likely to be a trade-off for the defending breeders between enhanced current reproductive success and possible injury or death and hence reduced residual reproductive value. Characteristics postulated to affect the brood defence cost: benefit ratio include parents' re-nesting potential, life expectancy, experience, sex and past parenting effort, and offspring age, stage of development, quality, vulnerability and brood size (Montgomerie and Weatherhead 1988). Although many of these postulated influences are difficult to test, some have been demonstrated convincingly (e.g. offspring age, number and quality, Curio 1987; offspring stage of development, Campobello 2008; parental sex and quality, Klvaňová *et al*. 2011 and Kryštofková *et al*. 2011).

The aims of this study were to determine:

(a) whether urban Little Ravens *Corvus mellori* select nest-trees non-randomly i.e. having distinctive characteristics. This was achieved by searching urban Melbourne for active nests, measuring their characteristics and comparing these metrics with those of systematically chosen control trees. I predicted that nest-trees would have characteristics distinguishing them from controls because Little Ravens in Melbourne are potentially at risk of clutch/brood predation, nest usurpation, brood parasitism and extra-pair copulations. Lill and Hales (2015) showed that in one season urban Little Ravens mainly nested in tall eucalypts, but did not analyse this trend further.

(b) which bird species entering the nest area do/do not elicit aggressive, defensive behaviour by nesting pairs of urban Little Ravens. It was predicted that many common species in suburbia would be ignored because they pose no obvious threat to nesting Little Ravens, but that potential nest predators, brood parasites and reproductive competitors would elicit brood defence.

(c) how this defensive spectrum compared with that of congeners. This was done by conducting a literature review, mainly of primary sources. The review was not exhaustive, but nor was it selective. The intention was simply to ascertain whether the targeting of brood defence in urban Little Ravens broadly resembled that in populations of exurban Little Ravens and urban and exurban congeners.

METHODS

Study species and area

Little Ravens are restricted to southeast Australia, from the Great Australian Bight to northeastern New South Wales. They occur in treed farmland, woodland, open forest and conurbations from the coast to alpine altitudes. The species is the numerically dominant *Corvus* species in Melbourne (Dooley 2012).

Nests were found by driving extensively around suburban Melbourne in three successive breeding seasons (June - December) searching for Little Ravens showing clear signs of nesting behaviour. The two closest nests studied were 225 m apart and the two most spatially distant ones were ~40 km apart.

Measurement of nest-tree and control tree characteristics

All nest-trees were identified to genus, but the genera *Eucalyptus* and *Corymbia* were lumped as 'eucalypts' (Wilson *et al*. 2005). Consequently, when presenting data on types of nest-tree used, the label 'groups' rather than genera is employed. I measured other characteristics of a subset of 88 nest-trees that were sufficiently accessible to permit such measurement. Distances were measured with a laser rangefinder and heights with a rangefinder and clinometer. The following measurements were made on this subset of nest-trees:

1 Height; height of the nest was also measured (both ± 0.1 m)

2 Maximum canopy diameter on North-South compass bearing (± 1 m).

3 Canopy cover, measured with *Canopy App* on a cell phone at 2 or 3 points below the canopy at my breast height and averaged. Higher values indicate greater canopy cover (i.e. a denser canopy).

4 Isolation index, the number of trees of similar height to the nest tree within 30 m of it.

5 Distance to nearest concealing cover (± 1 m), defined as a tree or built structure potentially offering nearly total concealment for potential nest predators. Pied Currawongs *Strepera graculina*, particularly, sometimes behaved cryptically around Little Raven nests.

6 Distance to nearest human food outlet (± 1 m); outlets were places where there was a potential for Little Ravens to access human food waste (e.g. cafes or large food stores with outdoor food waste bins etc.) (Yap *et al*. 2002; Lill and Hales 2015). This metric was obtained from *Google Earth* images.

A control tree was selected 100 m away from each nest-tree (100 m control) and the measurements detailed above were made on this tree for comparison. The rationale for this was that such a control was usually likely to be within the nesting pair's territory and in theory could equally have been chosen as the nest-tree. Ideally these controls would be chosen at random, but this was impracticable because many would have been inaccessible for measurement. Therefore, a systematic but unbiased selection process was used. On a Google satellite image of the nest site area, a 100 m control tree was selected by randomly choosing a main compass coordinate (N, S, E or W), drawing a straight line along that coordinate outwards from the nest-tree and selecting the tree intersected by the line at, or as close as possible to, 100 m. If there was no tree on or near the line about 100 m from the nest-tree, a second main compass coordinate was randomly chosen etc., until a control tree was obtained.

A second type of control tree was selected, a similar height control tree (SH control), namely the tree of similar height to each nest-tree within a 100-m radius of it that was closest to it. This was done for an unbiased sub-sample of 56 accessible nest-trees, although nine of them proved to have no suitable candidate SH control. Lill and Hales (2015) suggested that tall trees were preferentially chosen as nest sites by urban Little Ravens, so the rationale for these controls was to determine whether a tree of similar height in the chosen nesting area had other characteristics that made it less suitable for nesting. Again, the same set of measurements outlined above was made, but additionally I measured a coarse-grained Visibility Index for nest-trees and their paired SH control. This involved estimating whether there was a clear line of sight outwards horizontally for 100 m at nest height along the main compass coordinates (N, S, E and W). The index could thus range from 0 (no clear line of sight for 100 m on any co-ordinate) to 4 (unimpeded visibility over 100 m on all four coordinates).

Goodness-of-fit tests were used to examine disparity in: (a) taxonomic identity of nest-trees and their controls, and (b) response rates to intruders by nesting Little Ravens in the incubation versus the nestling stage. A series of paired samples *t* tests was employed to compare separately the characteristics of nest-trees with those of their individually paired 100 m and SH controls. Before conducting these tests, I determined that tree metrics were not inter-correlated. Data analysed by *t* test were checked for normality and homogeneity of variances; canopy cover was square root transformed. Sample sizes varied a little among tree metric comparisons, mainly due to varying accessibility for measurement.

Measurement of brood defence behaviour

Brood defence was studied mainly in one breeding season at a subset of all nests found that was chosen for visibility and to encompass a broad geographical spread within Melbourne. The closest two nests studied were 225 m apart and the two most widely separated nests ~21 km apart. Most brood defence observations (*BDOBS*) were made from a vehicle with tinted windows about 40 m from the nest-tree; the Little Ravens and intruders were clearly unaware of my presence. Observation sessions (58 to 185 minutes long, mean ~74 minutes) were conducted at various times of day from early morning to late afternoon, and overall at most nesting stages except nest building they were split evenly between morning and afternoon. No nest was observed more than once per day. The nesting birds could not be sexed or individually recognised.

I recorded intrusions by members of all bird species into a 40-m zone around the Little Ravens' nest-tree (or as much of it as was visible to me) and whether such intrusions entailed visiting the Little Ravens' nest-tree. The zone's radius was based on both visibility for the observer and my previous experience of Little Ravens' responses to birds near their nest-tree. I also recorded all aggressive interactions between the nesting ravens and these intruders and the outcome of these encounters. The one exception was that I did not record retaliatory aggression by intruding conspecifics, because this would have detracted from properly recording the nesting pair's defensive behaviour against them. Some intruders (mostly fast-flying, small birds) could not be identified to species and were designated 'unidentified'. The frequency of intrusions by birds did not necessarily reflect the actual number of individuals invading the nest zone, because some individuals continuously used the same space as the nesting Little Ravens and made repeated 'intrusions'.

Similar, limited observations of brood defence were also made at 4 nests observed primarily to record parental nest attendance (*PAOBS*) (Lill, in review). However, in these observations I only recorded intrusions into the nest zone and tree by, and responses of the breeding pair to, intruders to which the Little Ravens responded aggressively. There were 28 hours of such observations, 40.5% being pre-midday; they were spread across the incubation (44%), nestling (14%) and peri-fledging (42%) stages.

RESULTS

Nest site selection

Nest-trees (n=144) were found in public and residential gardens, streets, parkland, carparks, school grounds and golf courses. A bias towards streets and gardens was dictated partly by accessibility for the observer.

Tree groups used for nesting

Twelve tree groups were used for nesting by urban Little Ravens (Table 1); additionally, two nests were constructed on artificial structures (tall lamp posts). Eucalypts comprised 84% of nest-trees and no other tree group accounted for > 2.8%. In contrast, only 18.2% of the 100 m controls were eucalypts, and nest-trees and their 100 m paired controls (n= 88 pairs) were in different tree groups in 85.2% of cases (P < 0.0001, Binomial test). Among the 100 m controls, tree genera that were not used for nesting by urban Little Ravens included *Fraxinus*, *Grevillea*, *Kolreuteri, Melaleuca, Melia*, *Olea, Photinia*, *Pieris*, *Populus*, *Prunus, Pyrus, Quercus* and *Schinus.*

Table 1

Identity of Little Raven nest-trees and Similar Height control trees. Upper percentage for nest-trees is for total sample (n = 144), lower percentage in bold is just for nest-trees matched with an SH Control tree (n = 47).

Tree category	Percentage	
	Nest-tree	Similar height control tree
Eucalypt	84.0	
Eucalyptus/Corymbia	**83.0**	**74.5**
Norfolk Island Pine	0.7	
Auracaria		**2.1**
Cypress	2.8	
Cupressus	**2.1**	**4.3**
Cedar	0.7	
Cedrus	**2.1**	
Monterey Pine	0.7	
Pinus		
She-oak	2.8	
Casuarina/Allocasuarina	**8.5**	**2.1**
Plane	1.4	
Platanus	**2.1**	**8.5**
Elm	2.1	
Ulmus		
Fig	1.4	
Ficus	**2.1**	
Flame Tree	0.7	
Brachychiton		
Palm	0.7	
Phoenix		
Brush Box	0.7	
Lophostemon		
Oak		
Quercus		**4.3**
Silky Oak		
Grevillea		**2.1**
Poplar		
Populus		**2.1**

Mean distance between a nest-tree and its paired SH control was 31.3 ± 3.4 m, but 16.1% of nest-trees lacked an SH control within the specified area (Table 1). Nest-trees and their paired SH controls (n= 47 pairs) were in the same tree group in 74.5% of pairings (P = 0.001, Binomial test), mainly because eucalypts comprised ~75% of the SH controls. Although eight tree groups were represented in the control sample, only three of them (genera *Quercus*, *Grevillea* and *Populus*) failed to feature as nest-trees for urban Little Ravens.

Tree and nest height

The mean height of nest-trees was 23.3 ± 0.6 m (n = 83) and that of nests 18.0 ± 0.5 m (n = 79); the two metrics were positively correlated (Pearson $r_{(79)} = 0.877$, $P < 0.001$) (Fig 1). On average, nest-trees were about twice the height of their 100 m controls, whose mean height was 11.5 ± 0.7 m ($t_{(77)} = 13.621$, $P < 0.001$) (Fig 2a); they were numerically taller than them in 96% of nest-tree x 100 m control tree pairings, only 12.4% of which were eucalypt x eucalypt.

Tree canopy diameter and cover

Maximum canopy diameter and tree height were not correlated for nest-trees (Pearson $r_{(72)} = 0.210$, $P > 0.05$). On average, maximum canopy diameter was 1.7 x greater in nest-trees than in their 100 m controls (14.7 ± 0.8 versus 8.5 ± 0.5 m; $t_{(70)} = 9.065$, $P < 0.001$) (Fig 2b. 1). However, canopy diameter was similar in nest-trees and their paired SH controls, whose mean canopy diameter was 13.3 ± 0.8 m ($t_{(37)} = 0.945$, $P > 0.05$) (Fig 2b. 2).

Canopy cover was not correlated with maximum canopy diameter for nest-trees (Pearson $r_{(68)} = 0.027$, $P > 0.05$). Overall, mean canopy cover was 1.3 x greater in nest-trees than in their paired 100 m controls (41.1 ± 1.5 versus 32.1 ± 3.0%; $t_{(68)} = 4.226$, $P < 0.0001$) (Fig 2c. 1). However, canopy cover was similar in nest-trees and their paired SH controls, whose mean canopy cover was 43.1 ± 3.3% ($t_{(37)} = 2.012$, $P > 0.05$) (Fig 2c.2).

Tree isolation index

On average, nest-trees had fewer neighbouring trees of similar (or greater) height than did their 100 m controls (means: 1.2 ± 0.2 versus 5.2 ± 0.4 neighbours; $t_{(85)} = 11.331$, $P < 0.0001$) (Fig 2d. 1). Nest-trees also had fewer neighbouring trees of similar (or greater) height than did paired SH controls, whose mean was 2.0 ± 0.3 neighbours ($t_{(41)} = 3.315$, $P < 0.01$) (Fig 2d. 2).

Distance to concealing cover and nearest human food outlet

Mean distance to concealing cover was similar for nest-trees (18.1 ± 1.1 m) and their paired 100 m controls (19.6 ± 1.9 m) ($t_{(81)} = 0.694$, $P > 0.05$) (Fig 2e.1). Mean distance to the nearest human food outlet was also similar for nest-trees (395.4 ± 33.2 m) and their paired 100 m controls (367.6 ± 30.6 m) ($t_{(84)} = 0.335$, $P > 0.05$) (Fig 2f). Paired nest-trees and SH controls (mean 20.7 ± 2.1 m) were also a similar distance from concealing cover ($t_{(41)} = 0.485$, $P > 0.05$) (Fig 2e. 2). As most SH controls were found to be very close to their paired nest-tree, comparing their respective distances from the nearest human food outlet was redundant.

Tree visibility index

There was a 1.2 x greater mean estimated visibility over 100 m horizontally at nest height from nest-trees than from paired SH controls (2.7 ± 0.2 versus 2.2 ± 0.1; $t_{(41)} = 3.130$, $P < 0.01$) (Fig 2g). Estimated visibility was numerically greater from the nest-tree in 54% and from the paired SH control in just 8% of such pairings, 38% of pairings exhibiting no difference.

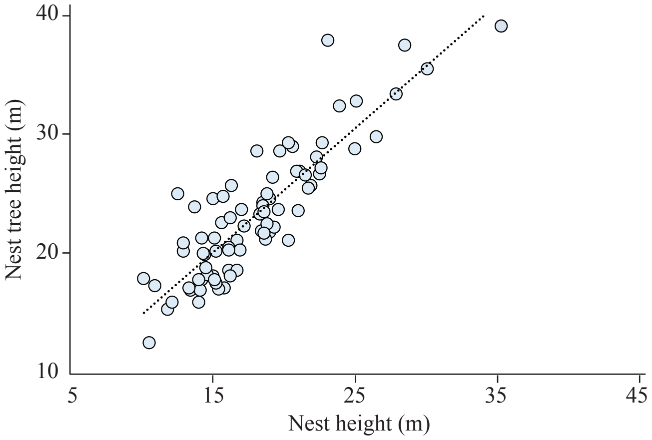


Figure 1. *Relationship between nest tree height and nest height for urban Little Ravens. Linear trend line is shown.*

Brood defence

Species entering Little Raven nest zones

Brood defence by urban Little Ravens against species invading their nest sites was monitored at 22 nests during ~113 hours of *BDOBS* covering all nesting stages. Additionally, it was documented on a more limited basis during 17 *PAOBS* sessions (Lill, in prep.) (see Methods).

In the *BDOBS* sessions, the mean rate of invading Little Raven nest-trees by birds (other than the nesting pair) was 6 intrusions/h; the mean rate of invading 40-m zones around nest-trees by birds and Domestic Cats *Felis catus* was 30 invasions/h. Nine identified bird species invaded Little Raven nest-trees, the most frequent being the Red Wattlebird *Anthochaera carunculata*, Noisy Miner *Manorina melanocepha,* Rainbow Lorikeet *Trichoglossus moluccanus* and Common Myna *Acridotheres tristis* (Table 2). Twenty-seven identified bird species invaded Little Raven nest zones and Domestic Cats entered two raven nest zones infrequently at ground level (Appendix 1, Table 2). No members of brood parasitic species entered Little Raven nest zones or trees.

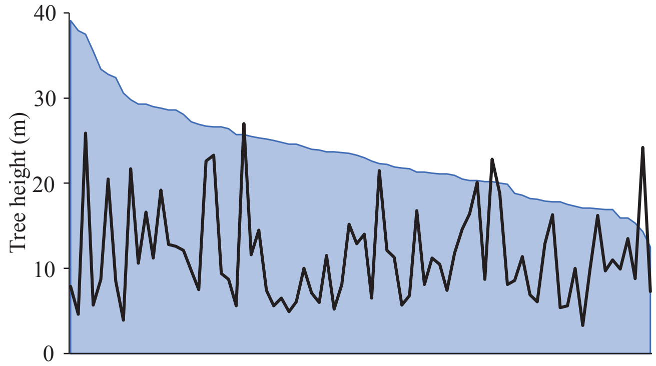
Species that elicited aggression in nesting Little Ravens

In *BDOBS* sessions, nesting Little Ravens responded aggressively to only four (44%) of the identified bird species that perched in, or flew through the canopy of their nest-trees, although at least one raven pair member was in the nest zone during 51% of the 568 nest-tree intrusions made collectively by these species (Table 2). Nesting Little Ravens only reacted aggressively to members of seven (26%) of the identified bird species that invaded their 40-m nest zones, although at least one pair member was present in the zone during 52% of the 2,552 zone intrusions made collectively by all intruding species (Table 2, Appendix 1).

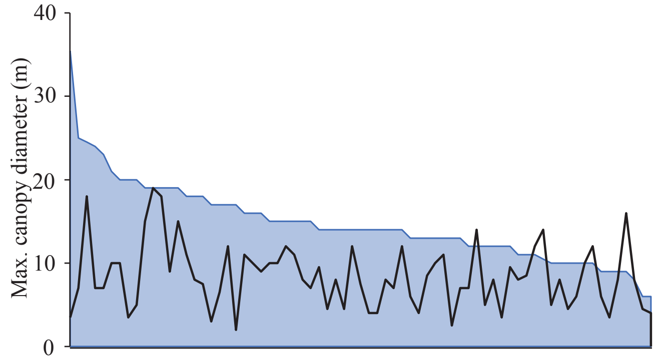
a. Conspecifics

At least one Little Raven pair member was at the nest site during 61% of intrusions by conspecifics. By far the greatest response rate by nesting ravens to any species was to these intruders, just over a third of whose intrusions elicited

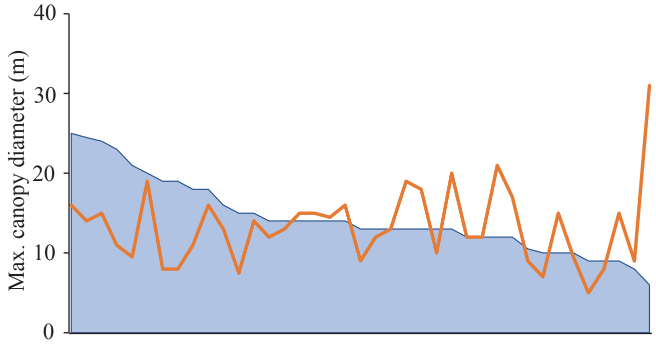
(a) Nest-trees x 100 m controls



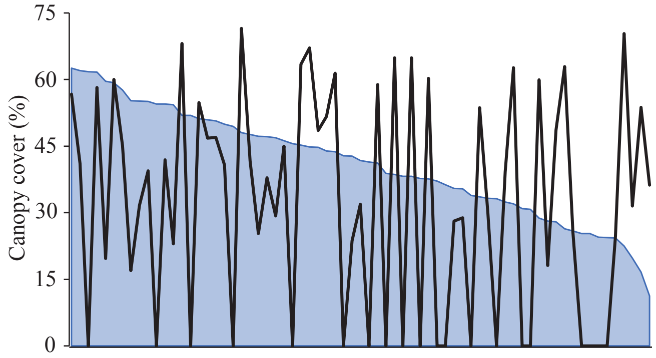
(b. 1) Nest-trees × 100 m controls



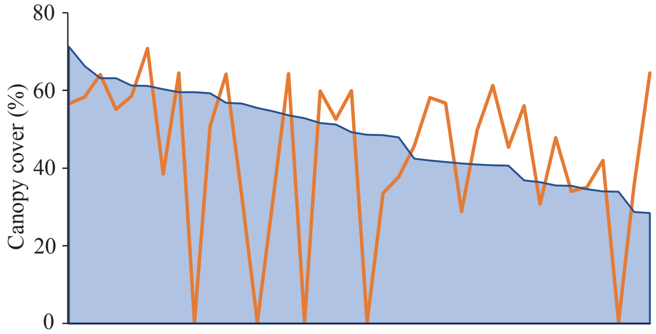
(b. 2) Nest-trees × Same Height controls



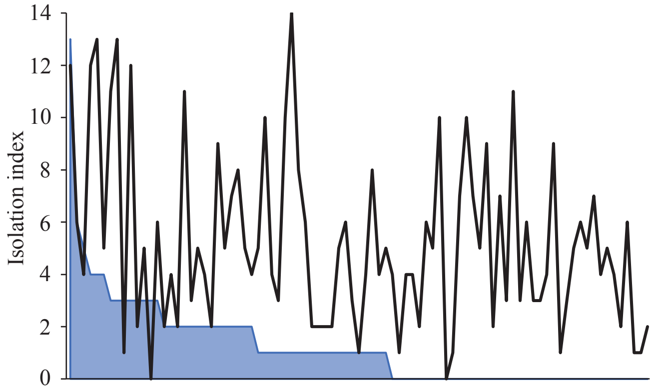
(c. 1) Nest-trees × 100 m controls



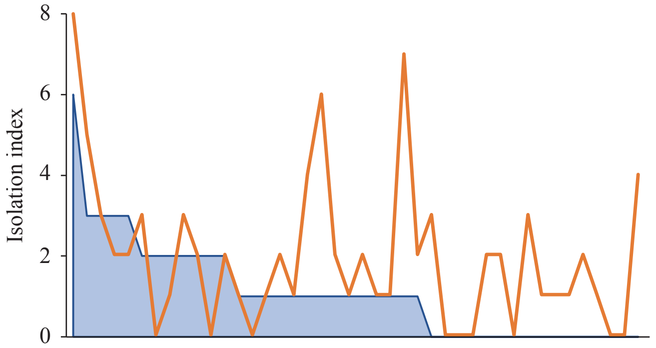
(c. 2) Nest-trees × Same Height controls



(d. 1) Nest-trees x 100 m controls



(d. 2) Nest-trees × Same Height controls



(e. 1) Nest-trees × 100 m controls

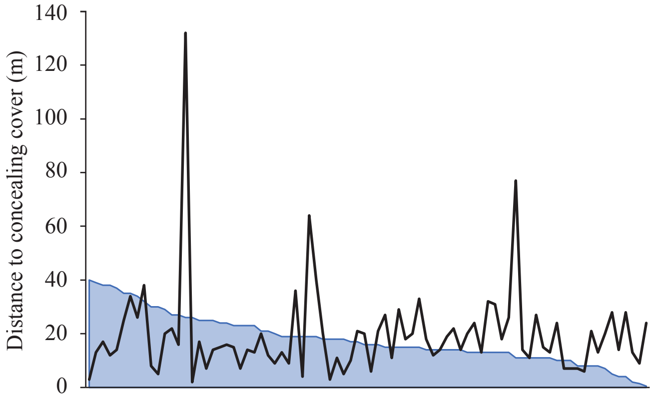
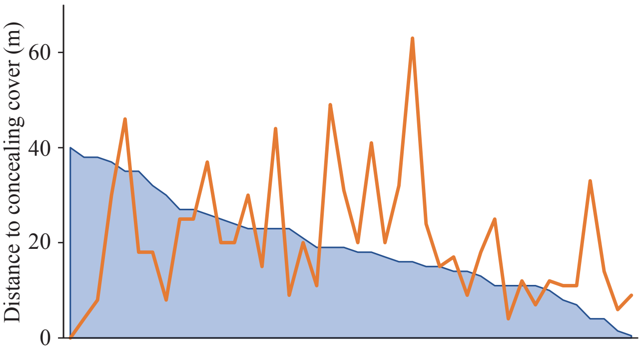
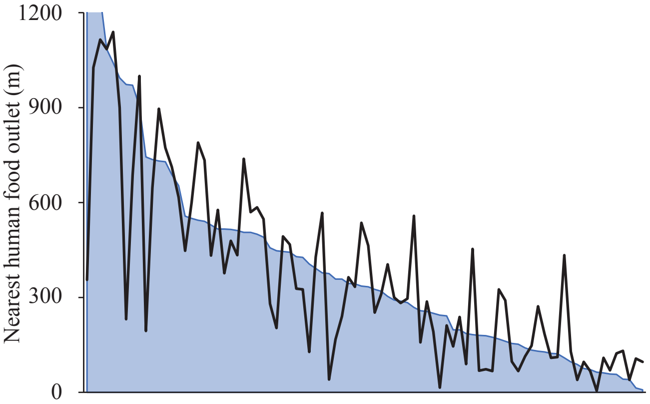


Figure 2. *Comparison of characteristics of urban Little Raven nest-trees and control trees. In all graphs, the nest-tree population is shaded in blue and ordered from the highest value for that variable on the left to the lowest on the right. The distributions of the paired controls are shown by a black line for 100 m controls and an orange line for the Same Height controls.*

(e. 2) Nest-trees × Same Height controls



(f) Nest-trees × 100 m controls



(g) Nest-trees x Same Height controls

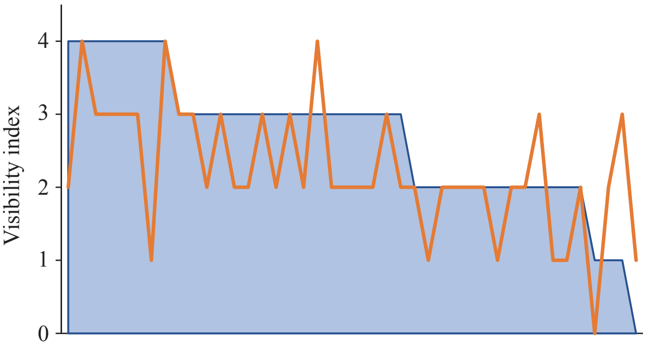


Figure 2 (continued). *Comparison of characteristics of urban Little Raven nest-trees and control trees. In all graphs, the nest-tree population is shaded in blue and ordered from the highest value for that variable on the left to the lowest on the right. The distributions of the paired controls are shown by a black line for 100 m controls and an orange line for the Same Height controls.*

aggression by at least one nesting pair member (Table 2). Nesting Little Ravens reacted aggressively to conspecific intruders at all breeding stages, but especially frequently during the nestling and peri-fledging stages, when around half of conspecifics' intrusions elicited nesting pair aggression. Often after aggressively chasing and expelling conspecifics from the nest zone, the breeding pair immediately returned to the nest-tree and performed wing-flicking calling displays (WFCD), possibly a sort of 'triumph display' in this context (Bigot *et al.* 1995). During *PAOBS* sessions, 46 conspecific intruders entered nest zones. At least one pair member was present on 98% of these occasions and 61% of the conspecific intruders were aggressively chased away by the nesting ravens.

Breeding pairs' responses to visible conspecifics well outside the nest zone were variable; sometimes they reacted overtly aggressively to them, sometimes they just performed WFCD in the nest zone, and often they showed no overt response to them, especially if they were clearly visible but more than ~100 m from the nest-tree. This response pattern was evident in both *BDOBS* and *PAOBS* sessions.

b. Currawongs

Pied Currawongs that entered Little Raven nest zones during *BDOBS* sessions elicited considerable breeding pair aggression. At least one nesting pair member was in the nest zone during nearly half of the currawong intrusions into ten nest zones and reacted aggressively on 23% of occasions (Table 2), always stimulating the intruder to flee. Similarly, during *PAOBS* sessions, when at least one Little Raven pair member was present during all 31 nest zone intrusions by currawongs, the ravens responded aggressively to only ~13% of these invasions. In contrast, although at least one raven pair member was also at the nest site during all 27 nest-tree intrusions by currawongs, the nesting bird(s) responded aggressively to 64.3% of them.

c. Magpies

During *BDOBS* sessions, at least one Little Raven pair member was present in the nest zone or nest-tree during nearly two thirds of the Australian Magpie *Gymnorhina tibicen* intrusions recorded, but reacted aggressively to only 11% of them (Table 2). The outcome of these encounters was less clear-cut, because magpies were also aggressive to the nesting raven(s) during some of their intrusions (Table 2). During *PAOBS* sessions, a further eight nest zone intrusions by magpies were recorded; although at least one nesting Little Raven was present on each occasion, no aggression towards the intruders was observed.

Collectively, for the three species to which nesting Little Ravens showed substantial aggression (conspecifics, currawongs and magpies), there was no difference in nesting birds' defensive response rates in their incubation and nestling periods (23.2% versus 31.6%, $\chi^2_{(1)} = 2.160$, $P > 0.05$).

d. Other intruders

During *BDOBS* sessions, a pair of nesting Little Ravens responded very aggressively to a Nankeen Kestrel *Falco cenchroides* that invaded their nest-tree, but without much obvious effect (Table 2). Nesting Little Ravens were in the nest-tree during nearly two thirds of Rainbow Lorikeets' entries and responded with low level aggression to 6% of them, although usually causing just local displacement. However, they did not respond aggressively during the lorikeets' nest zone intrusions which were 11.2 x more frequent, despite being in their nest zone during just over half of these intrusions (Table 2). Nesting Little Ravens also responded aggressively to intruding Noisy Miners, but to < 1% of their numerous intrusions. Red

Table 2

Agonistic interactions between breeding urban Little Ravens and birds invading the ravens' nest zone and nest-tree. Numbers in square brackets are the number of nest sites involved. Breeding stage indicated by NBO (nest building and oviposition), INC (incubation), NLG (nestling), P-F (peri-fledging) and UN (unknown). LR = Little Raven. Percentages of intrusions eliciting aggressive responses by nesting ravens italicized. Percentages of intrusions in which intruder was aggressive underlined. No percentages of intruders' aggressive responses given for Little Raven intruders (see Methods).

Intruding species	No. zone intrusions [no. nests]	% zone intrusions LR(s) present	% zone intrusions LR(s) aggressive	No. nest-tree intrusions [no. nests]	% nest-tree intrusions LR(s) present	% nest-tree intrusions LR(s) aggressive	% ALL intrusions when intruder aggressive
Nankeen Kestrel *Falco cenchroides*	**NLG: 1 [1]**	**100**	***100***	**0**			**0**
Galah *Eolophus roseicapilla*	INC: 14 [4]	100	0				0
	NLG: 8 [3]	37.5	*12.5*				0
	UN: 8 [1]	100	0				0
	TOTAL: 30 [6]	**83.3**	***3.3***				**0**
Rainbow Lorikeet *Trichoglossus moluccanus*	NBO: 41 [8]	34.2	0	19 [4]	68.4	*10.5*	0
	INC: 164 [11]	82.1	0	10 [1]	100	*10*	0
	NLG: 501 [12]	43.6	0	32 [6]	46.9	*3.1*	0
	P-F: 43 [5]	65.1	0	2 [1]	100	0	0
	UN: 49 [5]	16.3	0	5 [2]	0	0	0
	TOTAL: 762 [21]	**53.2**	**0**	**68 [8]**	**60.3**	***5.9***	**0**
Noisy Miner *Manorina melanocephala*	NBO: 73 [2]	41.1	*1.4*	40 [2]	27.5	0	12.4
	INC: 619 [6]	94.2	*0.2*	30 [5]	86.7	0	2
	NLG: 542 [7]	41.3	0	71 [5]	46.5	0	6
	P-F: 73 [3]	50.7	0	33 [2]	21.2	0	14.2
	TOTAL: 1307 [12]	**67.6**	***0.2***	**174 [9]**	**44.3**	**0**	**5.6**
Red Wattlebird *Anthochaera carunculata*	NBO: 50 [9]	14	0	37 [5]	43.2	*2.7*	0
	INC: 187 [9]	48.4	0	95 [9]	57.9	0	0
	NLG: 480 [12]	63.1	0	313 [11]	39.9	0	2.2
	P-F: 67 [4]	53.7	0	39 [4]	46.2	0	0
	UN: 69 [4]	21.7	0	12 [3]	50	0	0
	TOTAL: 988 [18]	**51.3**	**0**	**496 [15]**	**48.5**	***0.2***	**1.4**
Pied Currawong *Strepera graculina*	INC: 6 [2]	66.7	0	0			0
	NLG: 17 [5]	58.8	*29.4*	1 [1]	0		0
	P-F: 5 [3]	0	0	0			0
	UN: 7 [1]	28.6	*14.3*	0			0
	TOTAL: 35 [10]	**45.7**	***22.9***	**1 [1]**	**0**		**0**
Australian Magpie *Gymnorhina tibicen*	NBO: 8 [4]	37.5	0	1 [1]	100	*100*	11.1
	INC: 20 [5]	85	*10*	0			5
	NLG: 57 [12]	57.9	*7*	2 [2]	100	*50*	3.4
	P-F: 10 [2]	60	*20*	0			30
	UN: 35 [2]	62.9	*14.3*	0			0
	62.9	14.3	0				
	TOTAL: 130 [19]	**62.3**	***10***	**3 [3]**	**100**	***66.7***	**5.3**
Little Raven *Corvus mellori*	NBO: 25 [5]	68	*12*	0			
	INC: 73 [6]	83.3	*28.8*	0			
	NLG: 57 [11]	59.7	*49.1*	1 [1]	100	*100*	
	P-F: 28 [4]	96.4	53.6	0			
	UN: 4 [2]	100	*100*	0			
	TOTAL: 187 [17]	**76.3**	***38***	**1 [1]**	**100**	***100***	
Common Myna *Acridotheres tristis*	NBO: 73 [7]	43.8	0	4 [2]	75	0	0
	INC: 171 [8]	86.5	*1.2*	4 [1]	100	0	0
	NLG: 257 [11]	59.6	*0.4*	0			0
	P-F: 38 [4]	23.7	0	1 [1]	0	0	0
	UN: 56 [5]	44.6	0	0			0
	TOTAL: 595 [19]	**61.7**	***0.5***	**9 [3]**	**77.8**	**0**	**0**

Wattlebirds elicited Little Raven aggression during just one of their many intrusions into nest sites (Table 2), although during a *PAOBS* session I also observed a nesting raven displace a Red Wattlebird. Common Mynas stimulated brood defence by nesting Little Ravens in < 1% of their nearly 600 nest zone intrusions, and in none of their few nest-tree invasions. A Galah *Eolophus roseicapilla* elicited Little Raven aggression in one of the species' zone intrusions, the target bird fleeing in response to the threat (Table 2).

Actively incubating or brooding Little Ravens mostly did not overtly respond during *BDOBS* sessions to intruders of species to which they often reacted aggressively when off the nest. Only six instances of an aggressive response by an incubating or brooding raven were recorded in these sessions, five directed at intruding conspecifics and one at a magpie. Some of these intruders were in the nest-tree when the Little Raven pair-member vacated the nest to chase them. However, during *PAOBS* sessions currawongs entered the Fitzwilliam St nest-tree 27 times and the incubating female left the nest to aggressively chase them on 41% of these occasions.

Brood defence by other Corvus species

Information in the literature about the responses of nesting members of other Little Raven populations and other *Corvus* species to nest site incursions by vertebrates possibly constituting a threat to their breeding attempt is summarised in Table 3. Few authors list the species to which nesting ravens and crows do *not* respond.

The species that elicited aggressive defence by nesting members of other *Corvus* species are in 4 main categories: (a) raptors, including known predators of adult crows and ravens and their nest contents, and the main heterospecific usurpers of their nests, (b) other known nest predators (e.g. kookaburras, Australian Magpies and Domestic Cats), (c) large (e.g. cockatoos) and smaller (e.g. pigeons and honeyeaters) birds that seemingly pose little threat to nesting crows and ravens, and (d) conspecifics. The species that elicited defensive aggression in nesting rural Little Ravens were mostly in categories (a) and (d) (Rowley 1973), but in urban Albert Park in Melbourne they were in all four categories (Talmage 2011).

Aggression towards nesting Little Ravens by intruders

There was occasionally a little retaliatory aggression towards nesting pair members by intruding conspecifics being evicted from a Little Raven nest site. However, members of three other intruding bird species displayed more spontaneous aggression towards nesting Little Ravens, although the frequency was only substantial in Noisy Miners and Australian Magpies (Table 2). Miners and magpies were aggressive to raven pair members during ~6% and 5% of their intrusions, respectively. Red Wattlebirds were also aggressive to nesting Little Ravens, but during < 2% of their nest site intrusions in *BDOBS* sessions (Table 2). In *PAOBS* sessions, two further threats towards members of a Little Raven nesting pair by Red Wattlebirds were observed. Although no aggression towards nesting Little Ravens by intruding currawongs was witnessed in *BDOBS* sessions, one incidence was recorded during raven nest building in a *PAOBS* session, although it had little apparent effect.

SYNTHESIS AND DISCUSSION

Nest site selection

Urban Little Ravens predominantly built their nests in tall eucalypts that had few trees of similar (or greater) height nearby. Nest-trees had a broader and denser canopy than 100 m, but not SH, control trees. Visibility of the surrounding area at nest height was estimated to be better from nest-trees than from SH controls.

The observed predominance of eucalypts as Little Raven nest-trees in Melbourne replicated Lill and Hales' (2015) finding, suggesting that it was a stable trend over at least several years. That it involved choice rather than just being frequency-dependent was suggested by the high level of identity disparity between nest-trees and their paired 100 m controls and the diversity of tree groups among those controls. Little Ravens usually constructed their nests in the upper canopy of these eucalypts which, on average, were much taller than paired 100 m control trees. Nests that were not in tall eucalypts were usually in similarly tall trees belonging to other tree groups. Talmage (2011) found that Little Raven nests in urban Albert Park, Melbourne were mainly in Monterey Pines *Pinus radiata* and eucalypts, the most common tall trees at that location. However, pines constituted < 1% of nest-trees in my investigation.

The only likely nest predators potentially deterred by the substantial height of urban Little Ravens' nests would appear to be Domestic Cats. However, few cats were recorded in nest zones during (admittedly diurnal) observations and they did not elicit aggressive defence by nesting Little Ravens. The considerable height of most nests was conceivably most advantageous in enabling better surveillance from the nest for avian nest predators and competing conspecifics. This could have been augmented by the relative scarcity around the nest-tree of trees of similar (or greater) height that could restrict the view of the surrounding area from the nest. Due to the comparatively dense canopy of nest-trees, surveillance could also be conducted from the nest in relative concealment. However, given the alacrity with which absent parent Little Ravens sometimes returned to the nest site when potential nest predators invaded it, good visibility of the elevated nest area for parents foraging away from the nest site may be as important as outward visibility from the nest itself.

Boree *Acacia pendula* and Snow Gums *Eucalyptus niphophila* were the most frequent Little Raven nest-trees in Rowley's (1973) two rural study sites. He argued that rural Little Ravens probably did not use the nest as a 'lookout' because most nests in his study were only 3–9 m above ground level, whereas mean nest height in urban Melbourne was ~18 m in both the present investigation and that of Lill and Hales (2015). Mean nest height in Albert Park (15.5 m; Talmage 2011) was a little lower than that in the present study and that recorded by Lill and Hales (2015). Lee (2011) reported a mean nest height of 16.6 m for 21 urban Melbourne nests, again slightly lower than the mean height in the present study, but he also mentions some early records of much lower nests. Rowley (1973) deemed shading from sunlight unimportant in the placement of rural Little Ravens' nests, because they frequently built them in dead trees and on telephone poles. In contrast, only a few urban Little Ravens in my study built nests that were very exposed and

Table 3

Aspects of interspecific nest site defence by fifteen Corvus species derived from a search of largely original literature. Nest use relationship indicates that *Corvus* species uses old nests of the named species or vice versa. Grey shading indicates a lack of information.

Corvus species	Nest predators	Species involved in nest use relationship	Species against which nest site defended aggressively	Species tolerated at nest site without aggression	References
Pied Crow *albus*			Palm-nut Vulture (*Gypohierax angolensis*)		Lamm 1958
American Crow *brachyrynchos*	Raccoon (*Procyon lotor*) Great Horned Owl (*Bubo virginianus*) Grey Squirrel (*Sciurus carolinensis*)				McGowan 2001
		Black-crowned Night Heron (*N. nycticorax*) Coopers Hawk (*Accipiter cooperii*) Broad-winged Hawk (*Buteo platypterus*) Long-eared Owl (*Asio otus*) Great Horned Owl Mallard (*Anas platyrynchos*) Squirrel			Good 1952
Black or Cape Crow *capensis*			Jackal Buzzard (*Buteo rufofuscus*)		Skead 1952
Common Raven *corax*		Great Horned Owl Golden Eagle (*Aquila chrysaetos*) Red-tailed Hawk (*Buteo jamaicensis*)			Stiehl 1979
Carrion Crow *corone*			Rook		Coombs 1960
Australian Raven *coronoides*	Wedge-tailed Eagle (*Aquila audax*)	Black Falcon (*Falco subniger*)	Wedge-tailed Eagle		Rowley 1973
			Black Falcon		Debus *et al*. 2017
Chihuahuan Raven *cryptoleucus*			Swainson's Hawk (*Buteo swainsonii*) Northern Harrier (*Circus cyaneus*) Coyote (*Canis latrans*)		D'Auria and Caccamise 2007
Rook *frugilegus*			Carrion Crow Jackdaw Heron Wood Pigeon (*Columba palumbus*) Herring Gull (*Larus argentatus*) Buzzard (*B. buteo*) Peregrine Falcon (*Falco peregrinus*) Kestrel (*F. tinnunculus*) Sparrowhawk (*Accipiter nisus*) Eurasian Hoopoe (*Upupa epops*)		Coombs 1960
White-necked Crow *leucognaphalus*			Red-tailed Hawk Ridgway's Hawk (*Buteo ridgwayi*) Sharp-shinned Hawk (*Accipiter striatus*) Turkey Vulture (*Cathartes aura*) Hispaniolan Parrot (*Amazona ventralis*) Scaly-naped Pigeon (*Patagioenas squamosa*) Plain Pigeon (*P. inornata*) White-crowned Pigeon (*P. leucocephala*)		Wiley 2006

Table 3 *(continued)*

Corvus species	Nest predators	Species involved in nest use relationship	Species against which nest site defended aggressively	Species tolerated at nest site without aggression	References
Thick- or Large-billed Crow *macrorhynchos*			Raptors	Koel (*Eudynamys scolopaceus*) Sparrows (*Passer*) Bulbuls (*Pycnonotus*) Flycatchers Sunbirds	Lamba 1976
Little Raven *mellori* (rural)	Wedge-tailed Eagle	Nankeen Kestrel (*Falco cenchroides*)	Brown Falcon *(Falco berigoria)* Brown Goshawk (*Accipiter fasciatus*) Whistling Kite (*Haliastur sphenurus*)		Rowley 1973
(urban; Albert Park)			Little Eagle (*Hieraaetus morphnoides*) White-bellied Sea-Eagle (*Haliaeetus leucogaster*) Kestrel (presumably Nankeen Kestrel) Sulphur-crested Cockatoo (*Cacatua galerita*) Australian Magpie (*Gymnorhina tibicen*) Pacific Gull (*Larus pacificus*) Brush-tailed Possum (*Trichosurus vulpecula*)		Talmage 2011
Jackdaw *monedula*			Carrion Crow		Roell and Bossema 1982
	Pine Marten (*M. martes*)	Black Woodpecker (*Dryocopus martius*)			Johnsson 1984
	Stone Marten (*Martens foina*) Domestic cat (*Felis catus*)				Kaminski *et al.* 2015
	Common Raven (*C. corax*) Tawny Owl (*Strix aluco*) Least Weasel (*Mustela nivalis*) Brown Rat *(Rattus norvegicus)*	Stock Dove (*Columba oenas*) Tawny Owl			Madge and Burn 1994
Torresian Crow *orru*			Laughing Kookaburra (*Dacelo novaeguineae*) Grey Goshawk (*Accipiter novaehollandiae*)		Secomb 2005a
Fish Crow *ossifragus*			Coopers Hawk Common Grackle (*Q. quiscalus*)		McNair 1974
House Crow *splendens*			Raptors Koel Monkeys Domestic cat Snakes		Lamba 1976
Tasmanian Forest Raven *t. tasmanicus*			Grey Goshawk (*Accipiter novaehollandiae*)		Lawrence 2009
Northern Forest Raven *t. boreus*			White-bellied Sea Eagle Pacific Baza (*Aviceda subcristata*) Whistling Kite Brahminy Kite (*Haliastur indus*) Little Eagle Torresian Crow (*orru*) Eastern Rosella (*Platycercus eximius*) Noisy Friarbird (*Philemon corniculatus*)		Secomb 2005b

only 1.4% of nests were in artificial structures. Moreover, there was an indication that shade may be important for urban Little Ravens in that parents at a moderately exposed nest appeared to brood nestlings more on very sunny days (Lill, in review).

Nest heights and preferred nest-tree groups of the other four Australian corvids are: Australian Raven *C. coronoides*, rural, 12.2–8.3 m, 70% in eucalypts (Rowley 1973), and urban, mostly 10-25 m, 85% in eucalypts in northern and 62% in *Pinus* and *Auracaria* in southern Perth suburbs (Stewart 1997); Torresian Crow *C. orru,* rural, 12.2–15.2 m, 63% in eucalypts (Rowley 1973); Little Crow *C. bennetti*, rural, 6.1–9.1 m, 95% in Leopard Wood *Flindersia maculosa* (Rowley 1973); Tasmanian Forest Raven *C. tasmanicus tasmanicus*, urban and rural, mean 23.7 m (Lawrence 2009) and Northern Forest Raven *C. t. boreus*, rural, 23–36 m+ in coastal eucalypts (Secomb 2005a) and 18–21 m in tableland eucalypts (Debus and Rose 2006).

Collectively, these data suggest that both urban and rural Australian Ravens probably nest at a similar height to that used by Little Ravens in Melbourne. However, rural Torresian Crows, and particularly Little Crows, tend to nest at considerably lower heights, and rural and urban Forest Ravens mostly at greater heights than urban Little Ravens. More broadly, and not unexpectedly, there is great variation in nest sites of *Corvus* species and choice of site is not a conserved feature of their breeding biology.

Brood defence

Species eliciting little or no brood defence by Little Ravens

During *BDOBS* sessions, on average 30 hetero- and conspecific individuals intruded into Little Raven nest zones per hour, but only about a third as many species and one fifth as many individuals entered raven nest-trees. Although at least one Little Raven nesting pair member was in the nest zone or tree during just over half of these intrusions, < 2% of them elicited aggression by the nesting birds. There were two aspects to this low response rate:

1. Eighteen species (and unidentified birds) collectively made 2,006 intrusions without eliciting any Little Raven aggression (Appendix 1). This is not surprising given that only two of them, the Grey Butcherbird *Cracticus torquatus* and the Magpie-lark *Grallina cyanoleuca*, have been documented preying upon birds' nest contents (Major and Gowing 1994; Guppy *et al*. 2017). In the present study, butcherbirds were rare visitors to Little Raven nest sites, although Magpie-larks made nearly 100 invasions of raven nest zones and even a few of their nest-trees. Omnivorous urban Little Ravens consume soil and ground cover invertebrates, carrion and human food waste (Lill and Hales 2015), and inspection of Appendix 1 suggests that it contains few species with a similar diet to that of Little Ravens and likely to be major food competitors with them.
2. Collectively, five of nine species whose intrusions *did* stimulate aggression by nesting Little Ravens only elicited such behaviour very rarely *i.e.* on just 0.2% of occasions. For three of these species (Noisy Miner, Red Wattlebird and Common Myna), this seems a little puzzling at first because they are known to prey on birds' nest contents (Major and Gowing 1994; Fulton 2006). Moreover, in a *PAOBS* session in the present study a Noisy Miner that perched 3 m from a Little Raven nest during the nestling stage stimulated rapid return by the absent nesting pair, which expelled the intruder very aggressively. However, Noisy Miners, Red Wattlebirds and Common Mynas tend to be nest predators on species much smaller than the Little Raven. The low raven response rate to the other two species is understandable, as Galahs and Rainbow Lorikeets primarily eat plant components (although the lorikeets consume supplementary meat at feeding tables, Gillanders *et al*. 2017). However, again in a *PAOBS* session, a Rainbow Lorikeet that approached a Little Raven nest very closely was aggressively chased away by the incubating bird that left its nest briefly to do so.

Species eliciting substantial brood defence by Little Ravens

a. Currawongs

Breeding Pied Currawongs prey on eggs and nestlings of many bird species in urban and exurban environments (e.g. Priddel *et al.* 1995; Major *et al*. 1996; Prawiradilaga 1996; Bayly and Blumstein 2001; Fulton and Ford 2001; Guppy *et al*. 2017). They have colonised urban Melbourne progressively over the last approximately 30 years and thus now potentially pose a significant predatory threat to nesting Little Ravens in the city. During *BDOBS* sessions, currawongs entered Little Raven nest sites solitarily, and rarely invaded the nest-tree. Their intrusions were limited to only 45% of the monitored nest sites, at an overall rate of just 0.3 intrusions/h, although they intruded in all nesting stages except nest building.

Nesting Little Ravens responded aggressively to ~23% of currawong intrusions. Given that one or both raven pair members were at the nest site during nearly half of these intrusions, this means that they responded aggressively to only 47% of intrusions of which they must have been aware ('known intrusions'). This seems a rather low response rate, especially given that they were usually successful in displacing currawongs when they responded aggressively. However, no predation of Little Ravens' nest contents by a currawong was observed, although it was strongly suspected at the Fitzwilliam St nest observed during *PAOBS* sessions. This breeding attempt failed during incubation a day after multiple, simultaneous currawong invasions of the nest-tree that stimulated strong defence by both nesting ravens.

One factor contributing to Little Ravens' relatively low aggressive response rates to currawongs (and possibly magpies) could have been 'reluctance' of actively incubating and brooding individuals to leave eggs or young nestlings exposed, unless an intruder approached the nest very closely. Little Ravens had high incubation and early brooding attentiveness and typically left the nest unattended for only a few minutes during an unprovoked recess (Lill in review). During *BDOBS* sessions, incubating females left their nest to evict an avian intruder on just 3 occasions, once each for a currawong, a magpie and a conspecific that entered the nest-tree. Although high attentiveness is primarily important for maintaining optimal temperatures of embryos and ectothermic young nestlings (Deeming 2002), 'sitting tight' may also draw less attention by predators to incubating and brooding ravens than would vacating the nest to respond aggressively to them (Lawrence 2017), and consequently be particularly adaptive when the mate is absent. However, it was apparent in *PAOBS* sessions at the Fitzwilliam St nest that if currawongs approached a nest very closely, and especially if there was more than one of them present simultaneously, the incubating female would respond by leaving the nest, often several times in a few minutes, to try to aggressively evict them from the nest-tree.

b. Magpies

Australian Magpies prey on avian nest contents (e.g. Fulton 2006; Guppy *et al*. 2017), although the magnitude of their predatory impact may be less than that of currawongs and requires further clarification (Morgan *et al*. 2006). They are abundant in urban Melbourne (White *et al*. 2005) and during *BDOBS* sessions invaded Little Raven nest sites in all nesting stages, either solitarily or in small groups. They intruded much more extensively than did currawongs, being observed at 86% of nest sites monitored for brood defence and having an overall intrusion rate (1.2/h) 4 x that of currawongs. However, they too also mainly invaded nest zones rather than nest-trees. Nesting Little Ravens responded aggressively to 12% of magpie intrusions. Given that one or both raven pair members were present during 63% of these intrusions, this means that they responded aggressively to only 18.5% of the ‘known intrusions’. This seems a very low response rate if magpies constitute a significant threat to Little Ravens’ eggs and/or nestlings. Moreover, magpies may to some extent also be ecological competitors with Little Ravens, because they nest in quite similar situations (albeit often at a lower height), obtain much of their natural invertebrate food from the soil and ground cover, and consume supplementary food provided by humans (Jones 2018).

c. Conspecifics

Conspecific intruders visited Little Ravens’ nest sites at a rate of 1.7/h, respectively 1.4 x and 5.7 x more frequently than did magpies and currawongs. Nesting Little Ravens responded aggressively to ~38% of these intrusions. As at least one raven pair member was at the nest site during 76% of these intrusions, this means that they responded to just half of the ‘known intrusions’. Although this rate too seems rather low, it is a comparable response rate to that for ‘known intrusions’ by currawongs, but 2.7 x that for magpies. However, when considering Little Ravens’ low response rates to ‘known intrusions’ into their nesting territories by conspecifics, currawongs and magpies, it must be remembered that the magnitude of the parental and offspring factors thought to influence the cost-benefit equation underpinning brood defence decisions (Montgomerie and Weatherhead 1988) was mostly unknown in this study. The magnitude of these factors could conceivably help to explain the apparently low response rates of nesting ravens, and warrants detailed examination.

There are three main, plausible reasons for nesting Little Ravens responding aggressively to intruding conspecifics: (a) like many other *Corvus* species (e.g. Erikstad *et al*. 1982; Shields and Parnell 1986; Gaston and Elliot 1996; Carle *et al*. 2017), Little Ravens commonly prey on other bird species’ eggs and nestlings (Berry 2002; Ekanayake *et al*. 2015 a,b) and could conceivably prey on conspecifics’ nest contents (Davis and Dunn 1976), (b) intruding conspecifics may pose a threat in terms of extra-pair copulations, and (c) nesting ravens’ higher aggressive response rate to conspecifics than to currawongs and magpies may indicate that their intraspecific territoriality is primarily concerned with defence of limited optimal nest sites (and the food resources in the surrounding area required to sustain breeding). All three hypotheses are plausible. Intraspecific nest predation is believed to occur in Rooks *C. frugilegus*, Carrion Crows *C. corone* and some other *Corvus* species in Great Britain (Holyoak 1967; Coleman 1972; Tompa 1975) and extra-pair copulations have been documented in Rooks, American Crows *C. brachyrynchos*, Hawaiian Crows *C. hawaiiensis* and Common Ravens *C. corax* (Coombs 1960; Boarman and Heinrich 1999; HCWCS 2005; Townsend *et al*. 2010). As demonstrated above, Little Ravens select nest-trees with distinct characteristics and conceivably these trees are in limited supply and a source of intra-specific competition.

Hypothetically, nesting adults in altricial species should respond defensively more readily or intensely to intruders posing a threat to their breeding success during the nestling than the incubation stage; this is predicted because dependent offspring become more valuable in gene replication terms as they age (Montgomerie and Weatherhead 1988). However, such a disparity was not observed in Little Ravens’ responses to the intruder species to which they exhibited substantial aggressive behaviour.

Responses to raptors

Only two invasions of Little Raven nest sites by raptors were observed, one of which was around the nest-tree and elicited an aggressive response by a nesting pair member. This response was in one sense predictable because predation of Australian birds’ nest contents by raptors, such as goshawks, sparrowhawks and eagles, is well documented (Guppy *et al*. 2014), although to the best of my knowledge Nankeen Kestrels do not figure prominently among such records. They may constitute more of a threat of nest take-over than nest predation for Little Ravens, as they have been observed using old Little Raven nests (Rowley 1973; Table 3). Falcons, including small species such as the Australian Hobby *Falco longipennis*, are known nest usurpers of corvids and aggressive competition for nests and nest sites between Australian Ravens and raptors is well documented (Debus *et al*. 2017; Bauer and M^{c}Donald 2018; Morley in press).

Brood defence in other Corvus species

The major contrast between the species eliciting brood defence in most other studies of crows and ravens (mainly conducted in exurban environments) and those in Melbourne was that raptors featured minimally in my urban observations (Tables 2 and 3). Urban Albert Park, especially pre-modification to accommodate the Formula 1 Grand Prix, appears to be an exception to this disparity (Talmage 2011), possibly because it comprises 225 ha of parkland (including a lake) that may be more suitable for raptors than Melbourne’s residential suburbs. However, it is not entirely clear why birds-of-prey were so scarce in my observations, because many bird-hunting raptors have recently colonised and now thrive in urban environments worldwide (Kettle *et al*. 2017; Boal 2018; Kopij 2018). The absence of Pied Currawongs from Talmage’s (2011) inventory of species stimulating Little Raven brood defence in Albert Park is interesting, as they certainly occur in Melbourne’s southern suburbs.

Aggression towards Little Ravens by nest-site intruders

The two species that exhibited substantial aggression towards nesting Little Ravens, namely Noisy Miners and Australian Magpies, are well known for being very aggressive to other bird species (Jones 2002; Piper and Catterall 2003), although the reasons for this are not entirely understood. Some of the Noisy Miners involved were nesting within the ravens' nest site area, which would probably have enhanced their inherent, broadly-directed, aggressive tendencies because, as noted earlier, Little Ravens are nest predators. Red Wattlebirds are also quite aggressive to other bird species (Higgins *et al*. 2006), but were less aggressive towards nesting Little Ravens than miners and magpies. The most frequent type of aggressive behaviour towards nesting Little Ravens exhibited by heterospecific nest site intruders was threatening (including 'buzzing' – close aerial approach without physical contact); physical attack was rare, occurring 14 x less often than threatening. In most instances, nesting Little Ravens showed no overt response to such aggression; fleeing from the aggressor was very rare, occurring almost 30 x less often than a lack of an overt response. Thus, aggression by heterospecific nest site intruders had little effect on nesting Little Ravens, except for occasional minor disturbance.

Reproductive Effort

Nest sites had distinct characteristics, and although identifying an optimal site may not involve a huge time and energy expenditure by urban Little Ravens, it is likely to be crucial to breeding success. The substantial re-use of old nests would, of course, reduce the average RE expended on nest site selection. In contrast, defence of the nest and brood, especially against potential nest predators and competing conspecifics, appeared to be a substantial component of RE that is likely to have both significant benefits and costs for urban Little Ravens.

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Appendix 1

Bird species (and Domestic Cats) entering twenty-two 40 m Little Raven nest zones in urban Melbourne that did not elicit aggressive responses from the nesting birds. Numbers after each species in order are: number of intrusions [number of nest zones entered] and percentage of intrusions in which one or both breeding ravens were present in the nest, nest-tree or nest zone. The only species that visited the actual nest-tree were the Spotted Dove, Magpie-lark and some unidentified bird species. Species in taxonomic order by rows.

Silver Gull *Chroicocephalus novaehollandiae*	59 [6], 40%	Australian White Ibis *Threskiornis molucca*	12 [5], 0%
Little Corella *Cacatua sanguinea*	14 [5], 21.4%	Sulphur-crested Cockatoo *Cacatua galerita*	31 [1], 87.1%
Musk Lorikeet *Glossopsitta concinna*	4 [1], 100%	Eastern Rosella *Platycercus eximius*	5 [3], 80%
Rock Dove *Columbia livia*	451 [13], 45%	Spotted Dove *Spilopelia chinensis*	364 [17], 60.3%
Crested Pigeon *Ocyphaps lophotes*	6 [2], 66.6%	Welcome Swallow *Hirundo neoxena*	19 [6], 42.1%
Brown Thornbill *Acanthiza pusilla*	3 [1], 33.3%	White-plumed Honeyeater *Ptilotula penicillata*	4 [3], 100%
Little Wattlebird *Anthochaera chrysoptera*	1 [1], 0%	Black-faced Cuckoo-shrike *Coracina novaehollandiae*	2 [2], 50%
Grey Butcherbird *Cracticus torquatus*	2 [2], 50%	Magpie-lark *Grallina cyanoleuca*	96 [10], 57.3%
Common Blackbird *Turdus merula*	39 [9], 66.6%	Common Starling *Sturnus vulgaris*	262 [12], 65.7%
Unidentified raptor	2 [1], 100%	Other unidentified bird species	624 [22], 47.8%
Domestic Cat *Felis catus*	6 [2], 100%		