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Reproductive effort of urban Little Ravens: the nest attendance regime

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Parental care is a major component of reproductive effort in altricial birds, but the time allocated to it is patchily documented for *Corvus* species, including Little Ravens *Corvus mellori*. Nest attendance by Little Ravens was documented in urban Melbourne to: (a) assess its extent and potential to entail costs sufficient to significantly reduce its obvious fitness benefits, and (b) compare it with that of congeners, as reported in the literature. Both sexes built the nest and, on average, six 2-minute nest visits/hour were made during intensive nest building. Incubation was probably conducted exclusively or largely by the female, which was fed at the nest once an hour by her mate, whose visits lasted ~1 minute. Mean diurnal incubation attentiveness was 83% and there was a mean of 1.8 incubation bouts and 1.2 incubation recesses/hour. Both sexes brooded and fed the nestlings, although one sex (probably the female) appeared to do much more of the brooding after the first two weeks of nestling life. Mean diurnal brooding attentiveness considered over the nestling period *in toto* averaged ~20%, but it was as high as 75-90% early in development, before declining to close to zero. Provisioning of the brooding individual and/or nestlings occurred ~5.5 times/hour. When both nestlings and fledglings were present at the nest site around fledging time, they received an average of 7 provisioning visits/hour from parents. Nest attendance broadly resembled that of congeners, and overall was probably at a sufficiently high level to potentially have short- and long-term costs (as well as benefits) for parents.

INTRODUCTION

Reproductive effort (RE) is the proportion of an organism's total energy budget devoted to reproductive success. Life history theory predicts a trade-off between current and future reproduction; current reproductive success should increase and future reproductive success decrease as a function of increasing current RE (Stearns 1992). The trade-off is predicted because a high RE typically has a cost in terms of reduced adult survival or future fecundity (Hanssen *et al*. 2005), as it is likely to involve diversion of energy from growth and maintenance. Beneficially adjusting RE hinges on adult animals' ability to 'predict' the relative quality of a given breeding season for promoting growth and survivorship of young. Reproductive effort is expended in many ways, but in altricial birds is reflected strongly in the extent of parental care, as expressed in nest construction, incubation, brooding, and provisioning of nestlings and incubating and brooding adults. Quantitatively documenting this aspect of RE is one necessary step towards thoroughly understanding the hypothesised life history trade-off between current and future reproductive output in any altricial bird species.

Many aspects of breeding biology in the genus *Corvus* have been studied extensively (e.g. phenology, clutch and egg size, fledging success), but surprisingly, quantitative documentation of nest attendance is limited and patchy. Rowley's (1973) valuable pioneering study of four of the five native Australian *Corvus* species, Talmage's (2011) long-term study of Little Ravens *Corvus mellori* in a Melbourne park and investigations of native Forest Ravens *C. tasmanicus* by Secomb (2005a) and Lawrence (2009) have established the basic breeding biology of the Australian members of the genus, but there are still knowledge gaps and weaknesses, notably with respect to parental nest attendance. *Corvus* species' breeding biology is particularly interesting because it encompasses features of considerable theoretical significance. For example, incubation in most species is performed solely or largely by the female, who is provisioned by her mate. Whether the selection pressure influencing the male's rate of provisioning the female in such species is nest predation intensity, microclimate or food availability has attracted the attention of researchers trying to understand the selection pressures driving avian life history evolution (e.g. Martin and Ghalambor 1999; Conway and Martin 2000).

Our limited knowledge of Little Ravens' RE is based mainly on the work of Rowley (1973) for two rural New South Wales locations, Talmage's (2011) longitudinal data for a single urban park, and scattered information for other locations (Higgins *et al*. 2006). Although exploiting the abundant human food waste in cities (Lill and Hales 2015) may conceivably reduce the effort required to successfully rear young in urban environments, Little Ravens have a protracted pre-fledging development over ~59 days (Rowley 1973), so one would expect that the adults' total nest attendance levels would be high. This could have a negative effect on adult survival and future reproductive success unless other compensatory strategies occur (e.g. single broodedness within a season; Rowley 1973).

The aims of the present study were to:

(1) strengthen and broaden our knowledge of RE in Little Ravens, especially in the urban environment, by quantitatively documenting the nest attendance of breeding pairs widely dispersed in suburban Melbourne. I predicted that overall nest attendance levels would be high, given the protracted development of offspring.

(2) conduct an original literature search to facilitate comparison of nest attendance by urban Little Ravens with that of congeners in Australia and elsewhere. Avian nest attendance regimes vary geographically and between coexisting species with differing rates of nest predation risk, and they also exhibit intraspecific phenotypic plasticity in response to ambient nest predation risk (Martin and Briskie 2009; Chalfoun and Martin 2010). Given that the genus *Corvus* has a very broad geographical distribution, an underlying rationale for the literature search was to assess the extent to which this aspect of RE appears to be evolutionarily conserved or phenotypically plastic in the genus.

METHODS

Study species and area

Little Ravens are restricted to southeast Australia, from the Great Australian Bight to northeastern New South Wales. They inhabit treed farmland, woodland, open forest and conurbations from the coast to alpine altitudes. Rowley (1973) reported the duration of the incubation and nestling stages in rural New South Wales as 19–21 days and 37–38 days, respectively, and Talmage (2011) gives a mean nestling stage duration of 38 days (range 33–41 days) for Albert Park, Melbourne. The Little Raven is the numerically dominant *Corvus* species in Melbourne (Lee 2011; Dooley 2012).

Nests were found mostly by systematically driving around suburban Melbourne in three successive breeding seasons (June–December) searching for individuals showing clear signs of nesting. The closest two nests studied were 225 m apart and the two most spatially separated nests were about 21 km apart. Nests were mainly in suburban streets and residential gardens.

Nest attendance monitoring

Three points are pertinent with respect to the observation strategy:

(1) it mostly entailed watching several widely-dispersed nests at each nesting stage, mainly for just a few, relatively short sessions each, to provide a representative picture of nest attendance by Little Ravens in the city. The trade-off was that this strategy somewhat masked some trends (e.g. a developmental decrease in brooding attentiveness) that more long-term observation on particularly visible nests can document, although such observations were possible at a few nests.

(2) as I often could not clearly see the fine details of the behaviour that was occurring at the nest because of its height and the obscuring foliage (e.g. was a provisioning bird feeding just the brooding bird, the brooding bird and the nestlings, or just the nestlings?), the emphasis here is mainly on overall nest attendance patterns.

(3) because nests were too high up to permit inspection of contents, I often did not know how many young were present except at fledging. However, the number of nests studied at each nesting stage should be sufficient to encompass the natural variation in clutch and brood sizes.

Observations were made mostly from a vehicle with tinted windows about 40 m from the nest tree; the nesting ravens were clearly unaware of my presence. Sessions lasted 58–198 minutes (mean 74 minutes) and the ravens' activities were timed throughout a session. Observations were made from early morning to late afternoon, but were somewhat biased towards the morning and afternoon in the nest building and nestling stages, respectively. The sexually monomorphic ravens could not be sexed or individually recognised, but from observation and by analogy with Rowley (1973) some reasonable assumptions were made about some aspects of the sexual division of labour. Nesting stages had to be inferred from the birds' behaviour; any observations that could not be confidently ascribed to a stage were treated as 'unknown' in the analysis.

The following variables were measured, most frequencies being on a per hour (h) basis and durations in minutes (min):

[1] Nest building:

(a) frequency and duration of building visits and duration of intervals between consecutive visits during intensive construction.

(b) proportion of building visits that were by a single adult or the nesting pair.

Sessions that were known to be in the nest building stage, but in which no building behaviour occurred, were excluded from analysis.

[2] Incubation:

(a) diurnal incubation attentiveness (i.e. percentage of an observation session during which the presumed female incubated the eggs).

(b) number of complete and incomplete (i.e. wholly within and extending beyond an observation session, respectively) incubation bouts and recesses/h.

(c) duration of recesses occurring entirely within an observation session.

(d) frequency and duration of provisioning visits to the nest by the presumed male.

[3] Nestling:

(a) frequency and duration of provisioning visits to the nest by parents, and duration of intervals between consecutive visits.

(b) percentage of provisioning visits that were by just one parent (when little brooding occurred in a session).

(c) diurnal brooding attentiveness (i.e. percentage of a session during which nestlings were brooded) and the duration of brooding bouts.

(d) frequency of 'adventitious' nest building visits (see Results).

[4] Peri-fledging:

This period was defined as the time at which there were nestling(s) in the nest and sibling fledgling(s) in the nest tree or nearby or, less often, just fledglings in the nest tree and adjacent trees. Metrics recorded were:

(a) frequency and duration of provisioning visits to nestlings and fledglings, and duration of intervals between consecutive nestling provisioning visits.

Table 1

Nest building behaviour of Little Ravens at nine nests in urban Melbourne. Months abbreviated as Ju (June), Jly (July), Aug (August). Location of nests shown in top row: W St = Warra Street West, T H = Tramways Hotel, C St = Church Street, K Rd = Kooyong Rd, E Av = Elster Avenue, F St = Foch Street, G St = Goe Street, M St = Michael St and Wa Rd = Wallen Rd. Numbers in round brackets are standard errors and numbers in square brackets are sample sizes (nests or values). Summary column gives the means for all nests; no SEs are given because data are a mixture of 1 or 2 values and means for larger samples for nests. Number of sessions not indicated for nests individually for 'Mean no. nest building visits/h' because they are the same as in 'Minutes of observation'.

	W St	T H	C St	K Rd	E Av	F St	G St	M St	Wa Rd	Summary
Month(s)	Ju, Jly	Ju, Jly, Aug	Ju, Jly	Ju	Ju	Aug	Jly	Ju	Ju, Jly	**Ju, Jly, Aug**
Minutes of observation	183	180	247	186	246	60	60	73	313	**1,548**
[no. sessions]	[3]	[3]	[4]	[2]	[3]	[1]	[1]	[1]	[5]	**[23 sessions]**
Percent observation pre -12:00 hrs	100	33	49	100	100	100	0	100	100	**76.3**
Mean no. nest building visits /h	8.3	4.7	1.7	3.7	5.7	6	5	3.3	11	**5.5**
										[9 nests; 23 sessions]
Mean duration of nest building visits (min)	1.8	3.0	2.0	2.2	2.6	1	1	2	2.7	**2.0**
	(0.2)	(0.6)	(0.3)	(0.6)	(0.3)		(0.4)	(0.6)	(0.2)	
	[19]	[11]	[15]	[9]	[14]	[2]	[4]	[4]	[54]	**[9 nests; 131 visits]**
Mean interval between successive nest building visits (min)	9.4		13	15.7	16.8		18.7	2	3.6	**11.3**
	(3.7)		(2.9)	(4.0)	(4.5)		(3.8)		(0.6)	
	[15]		[6]	[6]	[7]		[3]	[2]	[31]	**[7 nests; 70 intervals]**

(b) frequency and duration of 'adventitious' nest building visits (see Results).

Where one or more nests contributed only one or two values for a measured variable, the grand mean for all nests and the mean of all the individual values for all nests for that variable were usually in close agreement, so only the former is presented. Variation among nesting pairs in the duration of nest visits and the interval between consecutive visits were analysed where possible (sufficient pairs with n ≥6) with single factor analysis of variance (ANOVA) after checking for data normality and homogeneity of variances.

The review of original, comparative data from the literature is not exhaustive, but neither is it selective. Many of the samples are small or narrowly-based, but collectively they provide a useful comparative framework. Studies in which helpers were involved in nest attendance have been omitted, as urban Little Ravens in my investigation did not exhibit this phenomenon.

RESULTS

Nest attendance

Nest building stage

Nest building was documented from early June to late September at nine nests in observations made predominantly before midday, as more building occurred in the morning (Table 1). The sample included new nests under construction and old nests being refurbished; these processes usually lasted two or more weeks. At this stage, the members of some pairs spent much of the day very close together, but members of other pairs were more independent in their movements. Both sexes built the nest. In the early stages, nest building ravens carried single twigs to the nest (including London Plane *Plantanus acerifolia, Eucalyptus* spp. and Queensland Brush Box *Lophostemon confertus*) gathered both close to (≤10 m) and well away from (>40 m) the nest tree. Sampling, by manipulation with the beak, to select an appropriate twig could sometimes take up to 5 min. Living twigs were detached from the tree with the beak and dead twigs were picked up from the ground, including ones that had been dropped during earlier construction. Little Ravens also transported moss, dry leaves and fine *Melaleuca* bark to their nest for the nest bowl and its lining. At some stages of building, twig and lining loads were interspersed both between and within the contributions of pair members. On some nest visits at this stage no material appeared to be transported to the nest.

Collectively, on average, during nest building the adults made ~6 nest visits/h; the sessional frequency ranged from 1.7 to 11 visits/h, reflecting the fact that building was sometimes performed in intensive bouts and sometimes more perfunctorily (Table 1). On average, building visits were short (~2 min), their duration being invariant among nesting pairs ($F_{5,116}$ = 1.871, P = 0.105), and consecutive visits were at ~8 min intervals. Visits to the nest site for building (n = 122) were variously: [a] solo (one pair member visited the nest on its own (57.4%), [b] overlapping (pair members arrived at the nest asynchronously, but nonetheless both were then present at the nest simultaneously) (19.7%), [c] synchronised (pair members arrived at the nest together) (13.1%), and [d] 'partially synchronised' (pair members arrived synchronously at the nest and nest tree, respectively, and one or both visited the nest, but if both did so it was asynchronously) (9.8%). The Kooyong Rd pair were seen performing courtship feeding once below the nest tree at this stage.

Oviposition stage

The egg-laying stage could only be observed with certainty at one nest. Observations (140 min) were made at this nest in two afternoon sessions in June and July. Copulation was observed twice in this pair, on a telephone pole and in a tree, both about 20 m from the nest tree. The pair made 3.2 visits/h to the nest, each lasting 2 min on average, and consecutive visits were about 13

Table 2

Parental nest attendance at twelve Little Raven nests in urban Melbourne in the incubation stage. Location of nests shown in top row; abbreviations as in Table 1, with addition of Con St = Constance Street, Oak Cr = Oakleigh Crescent, Cha Quad = Chatsworth Quadrant, St G Sth = St Georges Road South, Orr Rd = Orrong Road, Fitz St = Fitzwilliam St and LTU Bund = La Trobe University Bundoora Campus. Months abbreviated as in Table 2. Temporal spread of observations is the period (in days) from the first to the last observation. In data rows, numbers in round brackets are standard errors and those in square brackets are sample sizes (sessions or values analysed). Summary column for data rows gives mean for all nests; no SEs are given because data are a mixture of 1 or 2 values and means of larger samples for nests. * indicates two breeding attempts involved.

	Con St	K Rd	Oak Cr	Cha Quad	St G Sth	C St	E Ave	F St	Orr Rd	T H	Fitz St	LTU Bund	Summary
Month(s)	Sep, Oct	Ju, Jly	Aug	Sep, Oct	Aug	Jly, Aug	Ju, Jly	Aug	Oct	Aug	Sep	Sep, Oct, Nov	Ju to Nov
Observation mins [no. sessions] and temporal spread of observations (in days)	426 [8] 18	399 [7] 40	125 [2] 15	240 [4] 12	120 [2] 1	240 [4] 26	123 [2] 22	120 [1] 1	62 [1] 1	60 [1] 1	660 [6] 9	764 [10] 21*	Total 3,866 [52 sessions] 1–40 days
Percent observation pre-12:00 hrs	37.5	82.5	50	50	0	75	100	0	0	0	86.4	40.6	Mean 51.5
Mean incubation attentiveness (%)	74.9 (11.1) [8]	84.8 (5.3) [7]	72.6 [2]	97.1 [2]	89.2 [2]	81.7 [2]	100 [1]	91.7 [1]	66.9 [1]	57.5 [1]	95.8 (1.2) [6]	85.7 (4.3) [10]	83.2 [12 nests; 43 sessions]
Mean number of (complete and incomplete) incubation bouts/h	2.5 (0.3) [8]	1.9 (0.4) [7]	2.4 [2]	1.0 [2]	1.5 [2]	2.3 (0.3) [3]	1.9 [2]	1.0 [1]	1.0 [1]	2.0 [1]	1.7 (0.2) [6]	2.2 (0.2) [10]	1.8 [12 nests; 45 sessions]
Mean number of (complete and incomplete) recesses/h	1.7 (0.4) [8]	1.5 (0.4) [7]	1.6 [2]	0.5 [2]	1.0 [1]	1.0 [2]	0 [1]	1.0 [1]	1.0 [1]	2 [1]	0.8 (0.3) [6]	1.7 (0.3) [10]	1.2 [12 nests; 42 sessions]
Mean duration of complete recesses (min)	4.9 (1.0) [13]	6.9 (2.0) [8]	3.5 [2]	1.0 [2]		3.5 [2]		5.0 [1]		5.5 [1]	1.6 (0.3) [8]	5.7 (1.6) [18]	4.2 [9 nests; 56 recesses]
Grand mean provisioning nest visits/h	0 [8]	1.6 (0.5) [7]	0 [2]	1.3 (0.5) [4]	3.5 [2]	3.5 (1.3) [4]	1.9 [2]	2.5 [1]	1.0 [1]	1.0 [1]	1.3 (0.4) [7]	0.7 (0.3) [10]	1.2 [12 nests; 43 sessions]
Mean duration provisioning visits (min)		0.8 (0.1) [9]		0.7 (0.3) [5]	1.8 (0.5) [7]	1.2 (0.9) [13]	1.0 [1]	0.5 [1]		0.5 [1]	0.7 (0.1) [17]	0.5 (0) [5]	0.9 [9 nests; 59 visits]

min apart. Mean incubation attentiveness was very low (4.4%), reflecting the incompleteness of the incubation regime at this stage (e.g. Rowley 1973; Wang and Beissinger 2011).

Incubation stage

Incubation was documented at twelve nests from June to October in ~64 hours of observation (Table 2). By analogy with Rowley (1973), it was assumed that probably only females incubated, because no incubation change-overs were seen at nests where visibility was good.

Mean diurnal incubation attentiveness was 83%, and 72% of the individual sessional values were ≥80% (Table 2). On average, there were 1.8 complete (i.e. wholly within an observation session) and incomplete (i.e. extending beyond the observation session) incubation bouts/h and 1.2 complete and incomplete incubation recesses/h. Complete bouts lasted 24.9 ± 3 S.E. min (n = 43). However, the longest recorded complete bout (during a 3.1-hour observation session) lasted 109 min and 44.4% of incomplete bouts (n = 63) also lasted at least 25 min or considerably longer. The mean duration of complete (i.e. entirely within an observation session) incubation recesses was short (~4 min), but nine of 15 incomplete ones (i.e. extending beyond the observation session) exceeded this duration. The incubating bird was provisioned on the nest by her presumed mate 1.2 times/h on average, the mean duration of these visits being ~1 min.

Some incubating females exhibited ‘shaking’ behaviour, involving much rapid shaking of the wing and tail feathers. Its extent varied substantially among females, e.g. at the LTU Bundoora nest over 10 observation sessions (765 min), the incubating female ‘shook’ a mean of 0.9 ± 0.2 S.E. times/10 min of incubation, whereas the Fitzwilliam St female ‘shook’ a mean of 2.5 ± 0.7 times/10 min of incubating (7 sessions; 732

min). Some incubating females also frequently changed their orientation in the nest by at least 23° and up to 180°, sometimes in association with 'shaking'. The extent of this behaviour also varied considerably among females. Thus, the LTU Bundoora female made a mean of 0.8 ± 0.2 such orientation changes/10 min of incubation (10 observation sessions), whereas the Fitzwilliam St female only changed orientation a mean of 0.3 ± 0.3 times/10 min of incubation, and in five of seven observation sessions did not change orientation at all. Incubating females also occasionally spontaneously (i.e. in the absence of obvious disturbance) vacated the nest, perched briefly alongside it and then resumed incubating.

It was quite common in what appeared to be 'guarding' behaviour for the presumed male to spend a considerable amount of time perching prominently in the nest tree or nearby and sometimes performing wing-flicking calling displays (WFCD) while the presumed female incubated. Examples included:

(a) Kooyong Rd male – often perching prominently at the top of a bare tree 50 m from the nest tree for extended periods while the female was incubating, one such period lasting 9 min.

(b) Elster Avenue male – after provisioning the incubating female, once perched in the nest tree for 21 min, occasionally calling.

(c) Fitzwilliam St male – executed guarding bouts in the nest tree of 13 and 24 min duration on separate days, the latter bout including some 'perfunctory' arboreal foraging.

(d) LTU Bundoora male – habitually spent much time perching on a building 40 m from the nest tree while the female was incubating. One such bout lasted 12 min and another in a tree adjacent to the nest tree lasted 14 min.

Nestling stage

Parents' nest attendance during the nestling stage was documented at 15 nests in 75 hours of observation (Table 3a).

Provisioning visits:

Both parents fed the nestlings and, on average, there were 5.4 provisioning visits/h (range in nest means 1.9–8.2/h). On average, visits lasted just over 1 min and did not vary in mean duration among nesting pairs (with n ≥6) ($F_{11, 233}$ = 1.293, P = 0.229). Consecutive visits were a mean of 10 min apart, but the average interval between them varied 4.7-fold among nesting pairs (with an n ≥6) from 4.2 to 19.7 min ($F_{10, 155}$ = 2.599, P = 0.008). During this developmental stage in observation sessions when no brooding occurred, provisioning visits to the nest by parents (n = 100) were variously: [a] solo (81%), [b] synchronised (parents arrived at nest together) (10%), [c] overlapping (parents arrived asynchronously, but each visited the nest while the other was there) (8%), and [d] 'partially synchronised' (parents arrived synchronously at the nest and nest tree, respectively, but only one visited the nest) (1%). Feeding of one breeder by the other away from (~40 m) the nest was observed twice at the LTU Bundoora nest site during the nestling stage and was elicited by begging behaviour by the recipient. The recipient did not immediately fly to the nest, so it was unclear if this food was eventually given to, or shared with, the nestlings. This provisioning of the mate away from the nest could possibly be common in urban Little Ravens, but breeding adults were mostly out of my sight when not at the nest. Allopreening between the breeding pair away from the nest was observed twice during the nestling stage.

At the Kooyong Rd nest site parents approached the nest early in the nestling period through a series of short flights from branch to branch starting low in the nest tree, but later they nearly always flew directly to the nest. However, this was not a universal pattern, because the percentage of nest approaches that were directly to the nest at the LTU Bundoora nest was: day12, 80%; day 14, 100%; day 15, 40%; day 17, 43%; day 19, 37.5%; day 21, 25%; day 22, 80%; day 24, 75% and day 26, 75%. Over this period, 58% of nest approaches were directly to the nest (n = 45 approaches).

Brooding:

The mean duration of complete (i.e. wholly within an observation session) brooding bouts was ~14 min (range 2–60 min), but many incomplete bouts (i.e. extending beyond the observation session) were 15–60 min long. Diurnal brooding attentiveness averaged 19.6% over all observation sessions conducted at the nestling stage (Table 3a), but the average was slightly higher (23.1%) if only those sessions in which brooding was ongoing were considered. However, it must be emphasised that these data are averages for the entire nestling period. Observations at the particularly visible LTU Bundoora nest indicated that diurnal brooding attentiveness was 76–91% over the first six days of the nestling period, but declined to 15% by day 12 (Fig. 1). Thereafter it oscillated in a possibly weather-dependent manner (perhaps affected by ambient temperature and wind velocity) between 10% and 47% between days 13 and 21, before dropping to close to zero on day 23.

Over the first 17 days of the nestling period at the LTU Bundoora nest, both sexes brooded the nestlings. The percentage of brooding bouts that commenced with an identifiable change-over of birds was 40% on day 1, 14% on day 4, 25% on day 10 and 33% on day 17. On the intervening days and after day 17, no change-overs were observed. Change-overs could only be detected when one adult relieved its brooding partner and commenced a new brooding bout, as the sexes were indistinguishable. When an adult returned to brood when the nest was unoccupied (except for the nestlings), it was impossible to determine whether it was the same individual that had executed the previous bout of brooding. Both adults were present at the start of a brooding bout in only 32% of instances during that part of the nestling period in which change-overs were recorded. Identifiable change-overs occurred at the commencement of only 21% of brooding bouts in the 17-day initial nestling developmental period. Moreover, in two or three of the brooding bouts occurring after a change-over, the sitting bird seemed to be just covering the nestlings rather than actively brooding them. Therefore, it is at least conceivable that one sex (probably the female by analogy with Rowley, 1973) did most of the brooding overall.

Provisioning visits that took place when brooding was ongoing took various forms, including:

a) Visitor fed nestlings directly in presence of brooder.

b) Visitor just fed brooder.

c) Brooder departed when visitor arrived and visitor then fed nestlings directly.

Table 3a

Parental nest attendance at fifteen Little Raven nests in urban Melbourne during the nestling stage. Nest sites are shown in top row; abbreviations are as in Tables 1 and 2, with the addition of: Bke Rd N = Burke Rd North, Bel Rd = Belmore Rd, Koo Kt = Kooyongkoot Rd, Viv Ave = Vivianne Avenue, Sac St = Sackville St. Complete brooding bouts are those occurring entirely within an observation session. Numbers in round brackets are standard errors; numbers in square brackets are sample sizes (observation sessions or number of values analysed). Summary column for data rows gives mean for all nests. * observations spread over two breeding attempts by a pair.

Variable	Cha Quad	K Rd	Bke Rd N	E Ave	Orr Rd	Bel Rd	F St	Koo Kt	C St	War/ Pow	Oak Cr	Viv Ave	Sac St	St G Sth	LTU Bund	Summary
Month(s)	Oct/ Nov	Jly, Aug, Sep	Aug, Sep	Jly, Aug	Jly, Aug, Sep, Oct	Aug, Sep	Sep, Oct	Sep	Aug, Sep	Sep	Aug	Aug	Sep	Aug	Sep, Oct, Nov	Jly to Nov
Observation min [no. sessions] and below temporal spread of observations (days)	993 [10] 26	457 [6] 35	300 [4] 25	250 [4] 32	248 [5] 24*	183 [3] 34	181 [3] 28	180 [3] 11	147 [2] 15	137 [2] 14	120 [1] 1	60 [1] 1	60 [1] 1	60 [1] 1	1,257 [16] 27	Total 4,513 62 sessions 1- 35
Percent observations pre-12:00	6.1	47.5	73.3	100	51.6	67.2	33.1	100	57.8	100	100	100	100	83.3	19.0	Mean 38.3
Mean no. provisioning visits/h	1.9 (0.1) [10]	6.1 (0.4) [7]	5 (0.4) [5]	6.9 (1.1) [4]	6.5 (1.2) [4]	8.2 (0.9) [3]	6.6 (0.4) [3]	3.3 (0.7) [3]	5.5 [2]	5.9 [2]	5.0 [1]	5.0 [1]	8.0 [1]	3.0 [1]	4.0 (0.3) [16]	5.4 15 nests 63 sessions
Mean duration provisioning visits (min)	1.8 (0.7) [20]	1.3 (0.0) [35]	1.4 (0.7) [20]	1.6 (0.1) [22]	1.6 (0.0) [23]	1.0 (0.2) [19]	1.4 (0.1) [14]	1.0 (0.1) [6]	1.3 (0.1) [12]	1.8 (0.1) [16]	0.7 (0.1) [7]	1.0 (0.2) [5]	1.6 (0.1) [5]	2.5 (0.7) [3]	1.1 (0.2) [54]	1.4 (0.1) 15 nests 62 sessions 261 visits
Mean interval between successive provisioning visits (min)	19.7 (1.9) [8]	10.6 (0.4) [21]	6.7 (0.4) [13]	8.8 (1.0) [9]	5.7 (0.7) [17]	4.2 (0.5) [6]	8.9 (1.0) [9]	17 (1.5) [4]	10.9 (0.8) [7]	9 (1.4) [6]	10.6 (1.0) [6]	2.1 (0.4) [4]	2.0 [1]	19 [2]	14.0 (1.6) [59]	10.0 15 nests 53 sessions 172 intervals
Mean percent provisioning visits solo when <5% brooding attentiveness	0 [2]	46.1 (9.8) [4]	71.5 [2]	100 [1]	61.5 (18.0) [3]	100 [1]	62.5 [2]	69 [1]	66.7 [1]	100 [1]	100 [1]				50 [1]	63.9 12 nests 20 sessions
Mean brooding attentiveness (%)	50.6 (3.6) [9]	3.7 (0.9) [6]	25.7 (6.4) [5]	32.5 (13.0) [4]	7.2 (1.1) [5]	9.9 (4.0) [3]	20.9 [2]	21.7 (3.8) [3]	0 [1]	28 [2]	0 [1]		10 [1]		44.3 (7.4) [16]	19.6 13 nests 58 sessions
Mean duration of complete brooding bouts (min)	19.7 (5.3) [8]	6.8 [2]	13.4 (5.7) [5]	12.1 (3.4) [4]		11.8 [2]		19.5 [2]		20.5 [2]		20 [1]	6 [1]		13.4 (1.6) [35]	14.3 10 nests 62 bouts
Maximum duration of brooding bouts (min)	>59.5	7.5	36	>26.5	>13	14.6	25	20	>14	34		20			36	>59.5

d) Brooder sometimes departed nest with visitor when the latter had fed the young.

e) Brooder joined visitor in giving the food that the visitor had brought to the nestlings.

At the LTU Bundoora nest, parents starting brooding bouts in the absence of their mate fed the nestlings before commencing brooding on 82.4% of occasions.

The 'shaking' and changes of orientation observed during incubation also occurred during brooding. At the LTU Bundoora nest over the first 26 days of the nestling period, brooding birds 'shook' a mean of 1.1 ± 0.3 times/10 min of brooding (14 observation sessions; 539 min of brooding) and they changed orientation a mean of 0.5 ± 0.2 times/10 min of brooding (15 sessions; 539 min brooding). 'Shaking' occurred when feeding nestlings and at intervals during a brooding bout, and as during incubation was sometimes concurrent with orientation changes.

Other aspects of nest attendance during the nestling period:

At the LTU Bundoora nest faecal sacs were transported up to 40 m from the nest by parents until day 30 of nestling development. Occasionally, nest building was conducted by a

Table 3b

Parental nest attendance in the peri-fledging stage at nine Little Raven nests in urban Melbourne. Months abbreviated as Sep (September), Oct (October) and Nov (November). Nest identities shown in top row; abbreviated versions as in Tables 1, 2 and 3a. Numbers in round brackets are standard errors; numbers in square brackets are sample sizes (sessions or values analysed). Values in data rows in summary column are means for all nests.

Variable	Glenferrie Rd	E Ave	Glen Huntly Rd	Oak Cr	Sac St	Viv Ave	War/Pow Sts	Willis St	St. G Sth	Summary
Month	Sep	Sep	Nov	Sep	Sep	Sep	Sep	Oct	Sep	Sep, Oct, Nov
Observation mins (no. sessions)	99 [1]	60 [1]	444 [4]	60 [1]	60 [1]	65 [1]	60 [1]	64 [1]	70 [1]	Total 1,046 12 sessions
Percent observation min pre-12:00 hrs	0	100	66.2	100	100	0	100	0	100	Mean 54.7
No. nestling provisioning visits/h	4.9 [1]		2.3 (0.6) [5]	6 [1]	7 [1]	4.6 [1]	2.0 [1]	0.9 [1]	1 [1]	3.6 8 nests 12 sessions
Mean duration nestling provisioning visits (min)	2.0 (0.6) [5]		0.9 (0.3) [6]	1.5 [1]	0.5 (0) [3]	3.8 (2.6) [3]	6.5 [1]		3.5 [1]	2.7 7 nests 20 visits
Mean interval between nestling provisioning visits (min)	8.4 (2.3) [4]		11 (4.3) [6]	7 [2]	5.5 [1]	14.7 (4.2) [3]	13 [1]			9.9 6 nests 17 intervals
Mean no. fledgling provisioning visits/h		5 [1]		1.8 (2.2) [4]		3.8 (4.5) [3]	2 [1]	0.9 [1]		2.7 5 nests 10 sessions
Status of young during peri-fledging observation	One nestling and one fledgling 2m from nest	Two fledglings in nest tree and adjacent tree	Two nestlings in and out of nest; later, both fledglings perching in nest tree and nearby	One nestling and one fledgling in neighbourhood	One nestling and one fledgling in nest tree and adjacent tree	One nestling and one fledgling in nest tree	One nestling and one fledgling in nest tree		One nestling and one fledgling in nest tree vicinity	

breeding pair late in the nestling period (e.g. two nest-building visits in 60 min at the Orrong Rd nest at the late nestling stage). Late in the nestling stage, nestlings at most nests were active, clambering around the nest, perching on the rim and sometimes climbing out of the nest to perch nearby.

Peri-fledging stage

The peri-fledging stage was documented from September to November at nine nests during 17.4 h of observation divided evenly between morning and afternoon (Table 3b). Among these nests and over time at individual nests there were combinations of young ranging from one nestling in the nest plus one fledgling in the nest tree or nearby trees to 2 to 3 fledglings out of the nest and perching in the nest tree or adjacent trees. Provisioning visits to the nest by the parents at this stage averaged 4/h, all being brief (mean ~3 min). The mean interval between consecutive provisioning visits to the nest was approximately 10 min, although many intervals that apparently extended beyond the end of an observation session were substantially longer. The number of provisioning visits to fledglings (young out of the nest) at this stage averaged 2.7/h. When both nestlings and fledglings were present at the nest site, the number of provisioning visits to all the young collectively averaged 7/h.

At three nests, parents also performed substantial nest building at this stage, usually at the nest still in use or just vacated, but in one case in a nearby nest probably used by the pair in a previous season. Collectively, parents at two of these nests executed a mean of 4 nest building visits/h at this stage, interspersed with feeding nestlings and fledglings. These visits lasted 2.5 min, on average.

Brood overlap, re-nesting and out-of-season nest visits

There was one exception to the almost universal provisioning of incubating (presumed) females by their mates. In 7.1 hours of observation spread over 18 days, the incubating Constance St female was *never* provisioned by her mate. However, an adult, usually accompanied by a juvenile, was often present in the vicinity, the nest tree and adjacent trees. It often perched in an adjacent tree a few metres from the nest for considerable periods and sometimes performed WFCD there. It was observed several times defending the area against intruding conspecifics, and sometimes the incubating female joined it in this defence. She also occasionally joined the presumed male (and juvenile) in foraging near the nest tree. This appeared to be a clear example of brood overlap, but the presumed second breeding attempt failed late in the incubation stage due to an unknown cause. A second possible, but less certain, instance of brood overlap occurred at another nest.

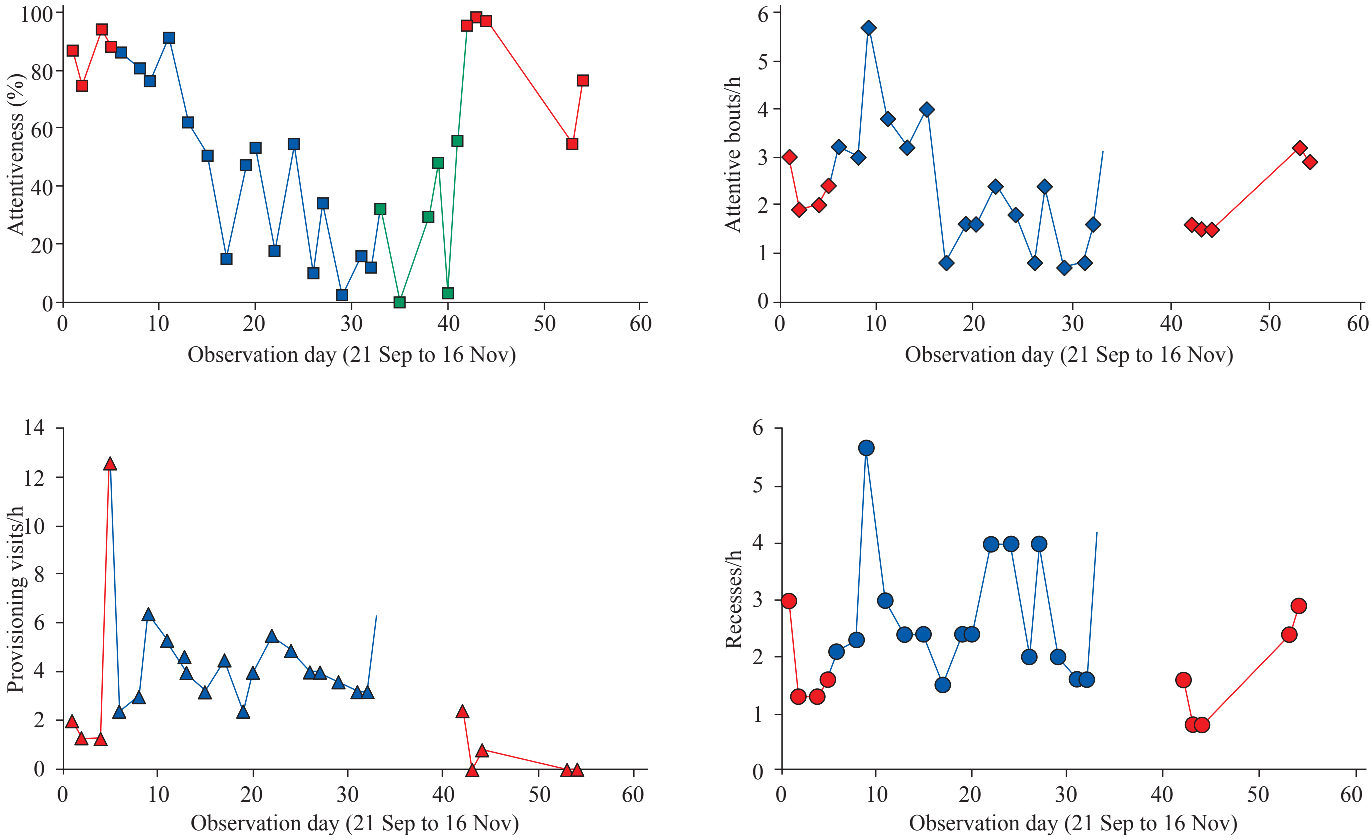

Figure 1. *Percentage attentiveness, provisioning visits/h, attentiveness bouts/h and recesses/h at the LTU Bundoora nest during a longitudinal sequence from incubation to brooding and then incubation again after breeding failure. Marker and line colours indicate: red, incubation stages; blue, nestling stage; green, "transition" from nestling to incubation stage. The green data points in the top graph were excluded from the summaries in Tables 2 and 3 because of their uncertain status, and are omitted from the other graphs in this figure for the same reason. The horizontal axis shows days since the inception of observation in the late incubation stage of the first breeding attempt. The only pronounced temporal trend was the decrease in percentage attentiveness during the brooding phase.*

Breeding pairs commonly re-used a nest that they had built (or probably built) in a previous season. However, when the Orrong Rd pair's first breeding attempt of the season appeared to fail soon after the peri-fledging stage, the pair was seen re-nesting 37 days later in a *different* nest in the same tree as the original nest, probably their own from a previous breeding season. The LTU Bundoora pair used the same nest twice during one season after their first breeding attempt failed at the nestling stage (Fig. 1). The second breeding attempt was initiated very soon after failure of the first, but it was impossible to accurately determine the exact interval between failure and re-laying. The second attempt failed at the incubation stage.

Adults visited nests in the non-breeding season. Some visits occurred within two months of fledging and included juveniles, but nest visiting by adults much further into the non-breeding season was occasionally seen too.

SYNTHESIS, COMPARISONS AND DISCUSSION

Nest attendance has not been widely documented for Little Ravens, but Rowley (1973) and Talmage (2011) provided valuable information for two rural and one urban location, respectively. Published information is more extensive for some of the other *Corvus* species in Australia and elsewhere (e.g. Butler *et al*. 1967; Rowley 1973; RØskaft *et al*. 1983; Secomb 2005a, b; Lawrence 2009) (Table 4). Nest attendance regimes vary among geographical regions and coexisting species with differing rates of nest predation risk (Badayaev and Ghalambor 2001), as well as intra-specifically in response to ambient nest predation risk (Martin and Briskie 2009; Chalfoun and Martin 2010). However, the nest attendance regime of urban Little Ravens broadly resembled that of both their rural counterparts (despite the probably greater food abundance in the city; Rebele 1994), and many other *Corvus* species globally. However, I saw no evidence of helpers-at-the-nest that have been described for a minority of *Corvus* species and populations (Verbeek and Butler 1981; Kilham 1984; Caffrey 1999).

Nest-building and egg-laying

The observation of nest-building being performed by both sexes of urban Little Ravens conforms with the pattern documented for rural populations (Rowley 1973), the Albert Park population in Melbourne (Talmage 2011), most other Australian *Corvus* species (Rowley 1973; Secomb 2005a, b; Lawrence 2009) and most congeners elsewhere (e.g. Lamm 1958; Stiehl 1985; Reaume 1987) (Table 4). Based on observation of colour-banded birds, Rowley (1973) stated that later in the building

Table 4

Comparative data on nest attendance for some *Corvus* taxa. A few values are expressed in the literature as per day rather than per hour and are so marked (/d). Durations are in minutes (min). Data are means, ranges or maxima. Values for certain times in a stage are indicated in square brackets. No data were found for the cells shaded grey. Sample sizes are given only for *C. mellori*. Albert Park and Langwarrin are in Melbourne, Victoria.

NESTING STAGE

Nest building:	Both sexes build	Female does most building later	Building visits/h	Duration of building visits (min)	Interval between successive building visits (min)	References
Pied Crow *albus*	✓		4.6 (but up to 12 in some obs. sessions)			Lamm 1958
Little Crow *bennetti*	✓	✓				Rowley 1973
American Crow *brachyrynchos*	✓		15–17	1.6 0.7-2.4	12	Reaume 1987
Black or Cape Crow *capensis*	✓					Skead 1952
Common Raven *corax*	✓	✓				Stiehl 1985
Australian Raven *coronoides*	✓		7 [early]			Rowley 1973
Rook *frugilegus*	✓	✓				RØskaft *et al.* 1983
Hawaiian Crow *hawaiiensis*	✓			7–12	2	HCWCS 2005 Tomich 1971
Mariana Crow *kubaryi*	✓	✓				Tomback 1986 Michael 1987 USFWS 2005
White-necked Crow *leucognaphalus*	✓			0.5		Wiley 2006
Large- or Thick-billed Crow *macrorhynchus*	✓					Madge and Burn 1994
Little Raven *mellori* (rural NSW)	✓	✓				Rowley 1973
(urban; Albert Park)	✓	✓				Talmage 2011
Torresian Crow *orru*	✓		8 [lining stage]			Rowley 1973
Fish Crow *ossifragus*	✓		9.2	1.9		McNair 1984
Forest Raven *t. tasmanicus & t. boreus*	✓		17–18	2.4–2.6		Secomb 2005a Lawrence 2009
House Crow *splendens*	✓	✓				Lamba 1976

process of rural Little Ravens the female does most of the actual building and the male just brings material to the nest, and similar divisions of labour have been noted in the Albert Park population and other *Corvus* species (e.g. RØskaft *et al*. 1983; Stiehl 1985; Talmage 2011). I could not determine whether this was true of urban birds generally, because I could not distinguish the sexes or often observe the fine details of behaviour at the nest. Sharing of nest building effort is probably important in permitting females to subsequently perform all the incubation. However, despite the shared nature of nest building, more than half of the building visits were by a single parent, as also reported for American Crows *C. brachyrynchos* (Reaume 1987).

Collectively, pair members made about six short building visits to the nest/h during intensive nest construction (Table 3). Comparable rates occur during early construction in Australian Ravens *C. coronoides,* at the lining stage in Torresian Crows *C. orru* and more generally in Pied Crows *C. alba* (Lamm 1958; Rowley 1973) (Table 4). However, much higher rates have been reported respectively for the Forest Raven *C. t. tasmanicus* (17–18/h; Lawrence 2009) and American Crow *C. brachyrynchos* (15–17/h; Reaume 1987). A visiting rate as high as these was only observed at one nest in one observation session in my investigation. However, the mean duration of nest building visits was similar (<2.6 min) in urban Little Ravens and all four species for which values are reported in Table 4. Rowley (1973) documented an equal sexual division of labour in Australian Ravens in the early stages and Torresian Crows in the later stages of nest building, but as noted above I could not distinguish the sexes in the Little Raven.

Forest Ravens sometimes add a few sticks to the nest wall around hatching time (Lawrence 2009) and I occasionally observed addition of nesting material during the incubation stage in urban Little Ravens. The substantial nest building observed in the late nestling and peri-fledging stages at a few Little Raven nests in my study and by Talmage (2011) at Albert Park has also been recorded for a pair of Australian Ravens (S. Debus pers. comm.). There are several plausible explanations for this intriguing behaviour in Little Ravens:

(a) urban Little Ravens often re-nest after a breeding failure (e.g. the Orrong Rd and LTU Bundoora pairs) (Talmage 2011), so this ‘adventitious’ nest building could be insurance against breeding failure soon after fledging. According to Rowley (1973), *Corvus* nests used for re-nesting after breeding failure are built (or re-furbished) much more rapidly than the original nest, underlining the urgency to commence a second breeding attempt.

Table 4 (continued)

Incubation:	By female only or mainly – fed by male	By both sexes	Provisioning visits/h	Interval between provisioning visits (min)	Duration of provisioning visits (min)	Incubation attentiveness (%)	Bout duration (min)	Recess duration (min)	Recesses/h	References
albus	✓					89 (Female: 77 Male: 12)	Female: 8-68; usually 10-25 Male: 2-6			Lamm 1958
bennetti	✓									Rowley 1973
brachyrynchos	✓							1-40		Good 1952
						46 [early] – 81 [late]		2-12	1-4	Kilham 1984
capensis		✓								Skead 1952
Northwestern Crow *caurinus*	✓		1.4			87		5.6		Butler *et al.* 1984
corax	✓		7/d					c. 10	0.2 [early] – 0.6 [late]	Stiehl 1979 Ratcliffe 1997
coronoides	✓		2				10-20			Rowley 1973
Chihuahuan Raven *cryptoleucus*	✓									D'Auria and Caccamise 2007
frugilegus	✓		1.3-1.6							RØskaft *et al.* 1983
			1.6-3.1	3-68						Coombs 1960
hawaiiensis	✓									HCWCS 2005
		✓				91	24.5	2.7	1.4	Tomich 1971
Taumalipas Crow *imparatus*	✓									Madge and Burn 1994
kubaryi	✓	Male gives minor assistance								Tomback 1986 Michael 1987 USFWS 2005
leucognaphalus	✓					96		5-15		Wiley 2006
macrorhynchus	✓									Kurosawa and Matsuda 2003 Lamba 1976
mellori (Albert Pk) (n = 2 sessions at different nests)	✓		2.6	22		96		3	0.3	Talmage 2011
Langwarrin (peri-urban) (n = 1 all-day session)			1.9	20		92		3	1.6	Thoday (cited in Talmage 2011)
NSW (rural) (n unknown)	✓									Rowley 1973
Jackdaw *monedula*	✓									Lockie 1955
			6.5							Henderson and Hart 1993
orru	✓									Rowley 1973
ossifragus	✓				0.6		31.5	3.8		McNair 1984
ruficollis	✓									Madge and Burn 1994
splendens	✓	(Male does ~ 33.3%)				89	126 (30-288)	18 (1-48) Male: 82 Female: 160		Lamba 1976
	✓	Male guards nest								Ranjan and Kushawa 2013

Table 4 (continued)

Nestling:	Brooding mainly by female	Both sexes brood	Brooding attentiveness (%)	Brooding bout duration (min)	No. brooding recesses/h	Brooding recess duration (min)	Provisionings of nestlings/h	Interval between provisioning visits (min)	References
albus	✓						2.9 [early] – 3.5 [mid] – 1.7 [late]		Lamm 1958
brachyrynchos	✓						3.8	15	Good 1952
									Caffrey 1999
caurinus	✓		93 [early] -18 [day 16-18]				2.7 [early] – 2 [late] Male: 1.8-0.8 Female: 0.9-1.2		Butler *et al.* 1984
corax	✓						45/d 102/d [mid] – 36/d [late]		Stiehl 1979
Hooded Crow *cornix*	✓		70 [early] – 25 [mid] – 0 [late]		10-20/d	1-5			Loman 1980
coronoides	✓		89 [early] – 33 [late]	39 [first 28 days]		8.3 [first 28 days]	1.1 [early] – 3.9 [late]		Rowley 1973
cryptoleucus		✓					9.4/h		D'Auria and Caccamise 2007
frugilegus	✓						1.4-3.3		Coleman 1972 RØskaft *et al.* 1983
hawaiiensis	✓								HCWCS 2005
leucognaphalus			84 [early] – 0 [mid-late]				5.1		Wiley 2006
macrorhynchos	✓								Kurosawa and Matsuda 2003
							13-16 [peak] to 2-5 [late]		Lamba 1976
mellori (Albert Pk) (n = 5 sessions at 4 nests)	✓		90 [early] – 0 [late]				3 [early] – 6 [late]		Talmage 2011
Langwarrin (periurban) (n = 1 all-day session)			54 [early-mid]				9 [early-mid] Male: 6 Female: 3	Male 10 Female 20	Thoday (cited in Talmage 2011)
NSW (rural)	✓								Rowley (1973)
monedula	✓								Lockie 1955
							6.5 [early/mid] – 13.5 [late]		Henderson and Hart 1993
orru	✓						3		Rowley 1973 Secomb 2005b
ossifragus	✓			*25*		*6*			*McNair 1984*
t. tasmanicus		✓							Lawrence 2009
t. boreus	✓		72-0 and 88-2	6-30			2-2.2		Secomb 2005a
splendens							16 [peak] – 6 [late]		Lamba 1976

(b) Forest Ravens sometimes build extra nests which are only used at night, possibly by roosting juveniles; however, unlike the situation in my study, such nests are built at the same time as the main nest (Lawrence 2009).

(c) Rowley (1973) states that the nest is sometimes used for nocturnal roosting by fledglings for a time after they depart from it. Conceivably the nest that is likely to be used by roosting juveniles sometimes requires running repairs to fulfil this function adequately, whether it is the one just used or an older one nearby.

Among Australian and many other *Corvus* species (and many other passerines), the eggs comprising a clutch are laid on successive days, except that one 2-day interval occurs somewhere in the laying sequence. Incubation is usually partial until several eggs have been laid (e.g. Emlen 1942; Skead 1952; Holyoak 1967; Rowley 1973). My observations at one urban Little Raven nest during egg-laying also suggested that the incubation regime was incomplete at this stage. Partial incubation is common in birds and may be functional in various ways, some of which do not require embryonic development to be initiated (e.g. preventing egg loss to predation, nest-site takeover or brood parasitism) and some which do (e.g. shortening the incubation period once the clutch is complete) (Wang and Beissinger 2011). Nest predation, and especially nest-site take-over by conspecifics, may well be threats to breeding urban Little Ravens (Lill, 2019). Partial incubation can also lead to asynchronous hatching in birds, which sometimes facilitates adaptive brood reduction in poor brood-rearing conditions (Stenning 2008).

Incubation

The female exclusively or mainly incubates the eggs and is fed by the male while she does so in most *Corvus* species studied, including rural and probably the Albert Park Little Ravens (*e.g.* Rowley 1973; Butler *et al*. 1984; Stiehl 1985; Lawrence 2009; Talmage 2011) (Table 4). However, in House Crows *C. splendens*, Thick-or Large-billed Crows *C. macrorhynchos*, Black or Cape Crows *C. capensis* and Hawaiian Crows *C. hawaiiensis* the male takes a minor role in incubation (Skead 1952; Tomich 1971; Lamba 1976). I assumed that exclusively female incubation happened in my study population because no incubation change-overs were observed during extensive observation at twelve nests, including two at which the details of activities at the nest were clearly visible.

Some incubating females frequently adjusted their orientation. These pronounced changes in orientation were not obviously concerned with egg turning and have been seen in congeners (e.g. Tomich 1971; McNair 1984). Lawrence (2009) has suggested for Tasmanian Forest Ravens that they may increase the efficiency of surveillance for predators and intruders, and this seems plausible for urban Little Ravens too. Female urban Little Ravens also ‘shook’ quite regularly, often without changing orientation. Although the bird’s focus seemed to be on the eggs during ‘shaking’, it was unlikely that they were turned each time that this behaviour occurred and conceivably some of these movements were concerned more with adequate heat transference to the entire clutch. However, it is unclear how shaking the wing and tail feathers would enhance such transference and the function of the behaviour requires further investigation, probably with fixed cameras.

Incubation attentiveness is an evolved trait, albeit with some phenotypic flexibility in relation to available food supply and nest predation intensity (Chalfoun and Martin 2007). Diurnal attentiveness in urban Little Ravens was high in my study and Talmage (2011) reports a comparably high level based on a small sample for Albert Park. The level of attentiveness was comparable with that of many north temperate passerines (Chalfoun and Martin 2007) and many other *Corvus* species, irrespective of their breeding latitude (Table 4). For Little Ravens in urban Melbourne, a high attentiveness is probably critical in maintaining an optimal embryonic temperature and growth rate (Deeming 2002) at prevailing low winter/spring ambient temperatures. Mean maximum and minimum monthly ambient temperatures during the three months in which incubation mainly occurred are 13.5–17.3°C and 6–8°C, respectively (Australian Bureau of Meteorology). Even the ambient temperature maxima are well below the commonly accepted physiological zero temperature for avian embryonic development (25–27°C) (Conway and Martin 2000a). High attentiveness may also be important in minimising the eggs’ visibility and exposure to nest predators and make their defence more efficient if the incubating bird is capable of repelling intruding predators, as in Little Ravens (Kleindorfer and Hoi 1987; Conway and Martin 2000b; Chalfoun and Martin 2007).

Incubation bouts wholly within an observation session typically lasted ~25 min., although some recorded during longer observation sessions and some that extended beyond the observation session were much longer. Rowley (1973) reports 10–120 min. durations for other Australian *Corvus* species and Lamm (1958) 8–68 min. durations for tropical Pied Crows (Table 4). Incubation recesses taken within an observation session were short (~4 min.) and comparable in duration with the mean values reported for Northwestern Crows *C. caurinus* and Forest Ravens (Butler *et al*. 1984; Lawrence 2009) (Table 4). However, some recesses taken by female urban Little Ravens that extended beyond the observation session were longer.

This kind of incubation regime, with high female attentiveness and (mostly) brief recesses, is facilitated by the male provisioning his incubating mate. This interpretation is supported by evidence that incubation attentiveness increases in uniparental incubator passerines as a function of the provisioning rate of the female by the male, at least up to an asymptotic rate of ~5 feeds/h (Martin and Ghalambor 1999). This relationship is thought to be influenced by nest predation intensity, because a high male provisioning rate is less likely to increase nest conspicuousness in a low than a high nest predation environment. On average, incubating female urban Little Ravens were provisioned by the male 1.2 times/h and similar rates have been reported for other Australian *Corvus* species, Northwestern Crows and Rooks *C. frugilegus* (Coombs 1960; Rowley 1973; Røskaft *et al*. 1983; Butler *et al*. 1984) (Table 4).

In some uniparental incubator species, the female is fed away from the nest by the male to some extent, which may adaptively reduce the nest predation risk by reducing nest conspicuousness (Lawrence 2017). Talmage (2011) observed such behaviour once at Albert Park. I did not observe it during the incubation stage in urban Little Ravens, but both sexes were out of my sight during many incubation recesses at most nests studied. If this behaviour is uncommon in *Corvus* species, their comparatively low male provisioning rates during incubation seem incompatible with the proposition that the nesting environment has a low nest predation intensity, as proposed for cavity-nesting passerines in Arizona, USA by Martin and Ghalambor (1999). Clearly, further targeted research is needed to decipher the major influences on the incubation regime in the genus *Corvus*.

'Guarding' behaviour was observed at several nest sites during incubation and was reported for Albert Park by Talmage (2011). It has also been recorded in Pied Crows, Common Ravens *C. corax*, Fish Crows *C. ossifragus* and Rooks (Lamm 1958; Coombs 1960; McNair 1984; Stiehl 1985) and seems likely to constitute surveillance for nest predators and/or conspecific competitors (Lill, 2019).

Brooding and provisioning nestlings

Altricial nestlings require brooding until they achieve endothermy, which is often substantially into the nestling period. Consequently, therefore, brooding attentiveness is high initially but declines during development. *Corvus* species exhibit this pattern, but in most of them the female alone broods the nestlings during their early development and is fed by the male while she does so (Table 4), although males do some brooding in some species (*e.g.* Forest Raven; Lawrence 2009). Rowley (1973) described brooding as being solely undertaken by the female in rural Little Ravens, but this was not the case in my study because I observed 6 change-overs at one particularly visible nest. However, male involvement in brooding may be fairly limited in urban Little Ravens, because these were the only change-overs observed in many hours of observation at 15 nests, including three at which the details of ongoing activity were clearly visible.

In urban Little Ravens, diurnal brooding attentiveness was ~20% over the entire nestling period. This figure is realistic, given that brooding attentiveness is initially very high but declines to a low level or zero in the second half of the (~38-day) nestling period, as documented for the LTU Bundoora nest in this study, Little Ravens at Albert Park, Australian and Forest Ravens and several *Corvus* species elsewhere (Lamm 1958; Rowley 1973; Loman 1980; Butler *et al*. 1984; Stiehl 1985; Secomb 2005a; Talmage 2011) (Table 4). The mean duration of brooding bouts that were completed within an observation session was 14 min., but many that started before or ended after an observation session were clearly much longer. Rowley (1973) reports a mean brooding bout duration of 39 min for the first 75% of Australian Raven nestling development and Secomb (2005a) bouts of up to 30 min. in Northern Forest Ravens *C. tasmanicus boreus* (Table 4). As with incubation, the high level of brooding attentiveness observed in *Corvus* species early in nestling development is probably facilitated by provisioning of the brooding bird by its mate. As happened during incubation, brooding Little Ravens exhibited 'shaking' and orientation changes. The function of 'shaking' during brooding and incubation is enigmatic, but the orientation changes during brooding may facilitate more efficient surveillance for predators and conspecific competitors. Certainly, brooding individuals indulged in much obvious visual surveillance of their surroundings.

Both urban Little Raven parents fed the nestlings, a pattern typical of virtually all *Corvus* species studied (Madge and Burn 1994), although feeding by the male is often done via the brooding female early in development in some species, including the Little Raven (Rowley 1973; Wiley 2006; Talmage 2011). Collectively over the entire nestling period, urban Little Raven parents fed their nestlings (and brooding mate) about 5–6 times/h, on average. Talmage's (2011) limited data for Albert Park equate to an overall rate of ~4 times/h. Frequencies of provisioning nestlings in some other *Corvus* species mostly appear to be a little lower than that in my investigation, although Pied Crows and White-necked Crows *C. leucognapthalus* may be exceptions (Table 4). Sixty to 70% of provisioning visits when brooding was not ongoing were solo visits. It has been suggested that synchronizing provisioning visits can be adaptive in reducing nest conspicuity to predators either by reducing 'traffic' at the nest site or calling by nestlings (Hall and Magrath 2011; Mariette and Griffiths 2012), but this was apparently either unimportant or not feasible in urban Little Ravens. Although Little Ravens cache food (Lill and Hales 2015), I did not observe any use of cached food in provisioning the nestlings, as reported for the species at Albert Park (Talmage 2011) and Northern Forest Ravens (Secomb 2005c), but it could have occurred out of my sight.

Urban Little Raven nestlings were very active towards the end of the nestling period, clambering onto the nest rim and even perching outside the nest, behaviour also noted in other *Corvus* species (e.g. Skead 1952; Lamba 1976; Wiley 2006; Lawrence 2009). Both Little Raven parents fed the young that were in and out of the nest through the few days of the peri-fledging stage. When a combination of nestlings and fledglings was present, the nestling(s) were fed collectively about 1.5 fewer 'meals'/h than the mean for the entire nestling period, but fledglings were also being fed a mean of 2.7 meals/h. Consequently, the overall rate of feeding young appeared to be slightly greater than that for the entire nestling stage. Of course, the parents' total workload at the three nests where 'adventitious' nest building also occurred at this stage was a bit greater again, although the nest building rate was 33.3% lower than in the true nest building phase.

Magnitude and costs of nest attendance

This study established that *in toto* urban Little Ravens exhibit a high level of nest attendance and parental care. On the average time-budgets documented, and allowing for the changing day-length during breeding and the differing time periods at which the breeding stages occurred, the following time expenditures can be approximately estimated:

a. Nest-building: would require a very substantial time (and energy) commitment by both sexes, but this is hard to quantify because of its discontinuous nature.

b. Incubation attentiveness: (calculated as mean incubation attentiveness × mean day or night length during main months when incubation occurred × incubation stage duration) – a female incubating throughout a complete incubation stage would spend an estimated 189 hours in diurnal and 291 hours in nocturnal incubation.

c. Provisioning of incubating female: (mean provisioning rate by male × mean day length in months when most incubation occurred × incubation stage duration) – during a complete incubation stage, a female would be fed by her mate an estimated 227 times (more if any substantial provisioning occurs away from the nest).

d. Brooding: (mean brooding attentiveness × mean day or night length in months when brooding mostly occurred × nestling stage duration) – parents that conducted a full brooding regime would brood the nestlings for an estimated 88 hours diurnally and 461 hours nocturnally. The latter number assumes that nestlings are brooded nocturnally right through until fledging, which was not definitely determined.

e. Provisioning of nestlings: (mean provisioning rate × mean day length during months of main nestling care × nestling stage duration) – a pair that provisioned each other (during brooding) and their nestlings throughout a complete nestling stage would collectively make an estimated 2,434 provisioning visits to the nest. It is not clear whether provisioning of one pair member by the other away from the nest adds to, or is incorporated in, this effort. There is a time commitment to faecal sac removal, but it is small.

f. Provisioning fledglings: parents feed the young for several weeks after they leave the nest (Rowley 1973).

Although it was beyond the scope of this inquiry, the energetic cost of egg-laying in Little Ravens must also be considerable because the most common clutch size of rural Little Ravens is four (Rowley 1973) and the mean egg dimensions of 44.4 × 29.9 mm translate into an egg volume of ~20 cm^3 (Hoyt 1979).

Incubation is critical, but involves a significant energy expenditure (Moreno *et al*. 1991; Tinbergen and Williams 2002) that can be reflected in immediate short-term costs to parents (e.g. reduced fledging success, Reid *et al*. 2002; reduced adult female mass, Hanssen *et al*. 2005). It may also be reflected in delayed costs, such as poorer survival to subsequent breeding seasons or lower future fecundity of the incubating birds (Visser and Lessells 2001; Hanssen *et al*. 2005). These costs are thought to occur because incubation's energetic cost must logically often be met by reallocating energy from other vital functions (e.g. immune competence; Hanssen *et al*. 2005). Brooding and provisioning nestlings are also energetically demanding activities; although these behaviours can strongly positively influence nestling growth rate (Henderson and Hart 1993), they can also have both immediate costs for the carers (e.g. reduced body condition; Dijkstra *et al*. 1990) and, as with incubation, longer-term fitness costs accrued through negative effects on their survival and future fecundity (Young 1996; Golet *et al*. 1998; Wernham and Bryant 1998). Such fecundity effects have been demonstrated experimentally in Rooks (Røskaft 1985). Thus, the high level of RE expressed in parental care, while increasing current reproductive success, may well have significant future fitness-reducing costs in urban Little Ravens.

Brood overlap and re-laying

Brood (or clutch) overlap occurs in a variety of bird species (Gru¨ebler and Naef-Daenzer 2010). It can potentially increase reproductive output when the breeding season is long relative to the developmental period of the young, the degree of cooperation between the breeders is high, and breeding associations are sufficiently stable and long-lasting for members to become experienced and efficient at breeding (Burley 1980). Although crows and ravens have high longevity and breeding pair membership is often stable over several breeding seasons, development is protracted (Marzluff and Angel 2005), which may be why brood overlap is uncommon (Rowley 1973). Unfortunately, the second breeding attempt of the Constance St pair failed late in incubation, so it was impossible to see how the female would cope with rearing a second brood after undertaking incubation in the first attempt without any provisioning by her mate. Talmage (2011) observed brood overlap at Albert Park, but all the second breeding attempts failed. This aspect of urban Little Ravens' breeding biology requires further investigation because it would be puzzling in such a long-lived bird if brood overlap is reasonably common but the second breeding attempts rarely succeed.

Re-laying within the same breeding season after breeding failure is well known for some *Corvus* species (e.g. Coleman 1972; Loman 1980; Stiehl 1985). However, Rowley (1973) found that it was uncommon in rural Little Ravens, but had been recorded up to 10 weeks after laying of the first clutch. Talmage (2011) reported that 80% of Albert Park pairs whose first breeding attempt of the season failed re-nested, and even 41% whose first attempt was successful re-nested. Judging from her behaviour, the Orrong Rd female appeared to re-lay about 9 weeks after her first clutch was laid and 37 days after the fledglings from this clutch disappeared. Interestingly, this female laid her second clutch in a different nest, but it was in the same tree as her first nest. If the first clutch was lost to predation, an adaptive shift in nest site might have been expected (Kearns and Rodewald 2013). Although it is very unlikely, I cannot entirely exclude the possibility that a different, late-nesting pair took over this nest tree. However, the LTU Bundoora female certainly laid a second clutch in the *same* nest that she used for her first breeding attempt of the season very soon after losing her brood to an unknown cause, although this clutch failed during incubation.

Future research

Knowledge of urban Little Ravens parents' nest attendance behaviour that requires further examination includes attendance during oviposition, attendance during the developmental decline in diurnal brooding attentiveness and the relative roles of the sexes in major attendance behaviours. Working out the last-named feature would require capture, genetic and/or morphological sexing and colour-banding of many individuals.

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