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To cite this article: Erin Cantor, Tamara Lewis, Marina Louter, Kevin Smith, Darren Schmitke, Claire Moore & Sonia Kleindorfer (2019) Nest site attributes and nesting outcome in the vulnerable eastern Regent Parrot (*Polytelis anthopeplus monarchoides*), Transactions of the Royal Society of South Australia, 143:1, 147-165, DOI: 10.1080/03721426.2018.1552825

To link to this article: https://doi.org/10.1080/03721426.2018.1552825

Published online: 11 Dec 2018.
Nest site attributes and nesting outcome in the vulnerable eastern Regent Parrot (*Polytelis anthopeplus monarchoides*)

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**ABSTRACT**

The relationship between nest site characteristics and nest success is likely to be important in the conservation management of threatened cavity-nesting birds. The vulnerable eastern Regent Parrot (*Polytelis anthopeplus monarchoides*) is declining in South Australia, but there is little information on the behavioural ecology of its cavity-nesting habits. The aim of this study was to quantify parental nest visitation behaviour and measure nest site attributes in relation to nesting outcome. We collected data from 25 nests along the Murray River in South Australia, and analysed 608 h of video recording and 67 h of binocular observations. This study provides the first quantitative data on parental care behaviour of the eastern Regent Parrot. The results show (1) parent birds had ~0.5 visits per hour during incubation and ~2 visits per hour during feeding; (2) 16% of nesting cavities were abandoned, 24% usurped, 4% depredated (by lace monitor, *Varanus varius*), 4% unknown outcome; and (3) canopy cover was 58% at successful nests versus 34% at failed nests. Behavioural monitoring in the field should span at least two hours to capture parental activity at the nest, nesting success was correlated with canopy cover, and nesting failure was mostly explained by usurpation and abandonment.

**Introduction**

Biodiversity is declining at the highest rates since human record-keeping began (Olah et al., 2016). Species extinction is often associated with habitat loss or modification (Owens & Bennett, 2000). Of the ~10,000 extant bird species, around 1200 are declining (IUCN, 2018; Rodrigues, 2006). Therefore, understanding the role of habitat parameters for reproductive success in vulnerable species can be an important component of successful conservation management (Ford, Walters, Cooper, Debus, & Doerr, 2009). Birds are useful bioindicators of functioning ecosystems and their response to ecological variables can be explored to ensure their persistence in ecosystems (Schulze et al., 2004; Carignan & Villard, 2002; Segura, Castaño-Santamaria, Laiolo, & Obeso, 2014).
Parrots (Psittaciformes) provide multiple ecological services, including a role as genetic linkers, seed facilitators for secondary dispersers, and plant protectors (Blanco, Hiraldo, Rojas, Dénes, & Tella, 2015). Given their charismatic appeal and their high extinction risk (Olah et al., 2018), parrots are often used as a flagship species for conservation (Douglas & Verissimo, 2013; Leader-Williams & Dublin, 2000). Of the 397 parrot species, ~110 species are threatened globally according to BirdLife International (2014) (cited in Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015). Parrots are often large bodied and slow breeding, and 70% of them are ecologically specialized. All of these traits are associated with increased extinction risk (Olah et al., 2016). In addition to these life history traits, most parrots are secondary cavity nesters that depend on existing cavities for nesting (De Labra-Hernández & Renton, 2016; Renton et al., 2015). Parrots occur primarily in tropical and subtropical environments as well as temperate climates in southern Australia and New Zealand (Koutsos, Matson, & Klasing, 2001). Australia has 54 species of parrots, 15 of which are currently threatened (Olah et al., 2018). The main threats to Australian parrot species have been identified as competition from invasive species, over-abundance of parrots, habitat loss due to agriculture, hunting and trapping, and disease (Eastwood et al., 2014; Olah et al., 2018). In general, more field study is needed to understand mechanisms of habitat selection and causes of nesting failure in Australian parrot species at risk of extinction (Olah et al., 2016).

Nesting success is a key component of avian fitness, from which one can infer parameters of population viability (Cockle, Bodrati, Lammertink, & Martin, 2015). Of course, post-fledging survivorship is another key variable to predict population viability. In general, cavity-nesting birds have larger clutches and lower predation risk than cup-nesting birds (Cockle et al., 2015; Martin & Li, 1992). Despite overall benefits of cavity-nesting from lower predation risk and stable thermal environment, the cavity can vary in characteristics important to the nesting bird (Rendell & Robertson, 1989) and birds are sometimes forced to occupy suboptimal cavities where they experience lower success (Stojanovic, Rayner, Webb, & Heinsohn, 2017). Determining how nesting success varies with cavity characteristics is important for the conservation of cavity-nesting species, particularly because tree cavities are increasingly limited (Manning, Gibbons, Fischer, Oliver, & Lindenmayer, 2013). The nesting success of cavity-nesting birds has been shown to be affected by canopy cover (Deng & Liu, 2015), canopy connectedness (Koenig, Wunderle, & Enkerlin-Hoeflich, 2007), cavity morphology including height above ground, entrance diameter, and depth (Bourgeois & Vidal, 2007; Cockle et al., 2015; Evans, Lank, Boyd, & Cooke, 2002), and parental care (Berkunsky et al., 2016). Because the relationship between nest site characteristics and nesting success might differ between species, each species requires its own study.

Nest predation is a major cause of nesting failure and shapes avian life histories (Weidinger, 2002). Birds have evolved direct anti-predator strategies such as active nest defence (e.g. direct attacks, mobbing and guarding), or passive defence, including nest site selection or concealment of nest contents (Komdeur & Kats, 1999; Weidinger, 2002). Parental care behaviour can enhance nest survival through nest defence behaviour, but it can also disclose information about nest location (Remes, 2005; Weidinger, 2002). Numerous observational and experimental studies have demonstrated that parental care behaviour at the nest can be a cue for predators (Gottfried & Thompson, 1978; Grant, Shaffer, Madden, & Pietz, 2005; Martin, Scott,
Cavity-nesting species provide an interesting opportunity to test effects of parental care behaviour on nest predation because nest contents are visually concealed. Skutch (1949) hypothesized that increasing parental activity at the nest would increase nest predation. Parental provisioning requirements vary throughout the breeding season from incubation to feeding, and generally parents increase their nest visitation rate during nesting, because chicks require more food as they grow (Martin et al., 2000). Increasing nest visitation rates during nesting could result in higher predation risk (Eggers, Griesser, & Ekman, 2008). Most parrots nest in cavities, and predation risk in cavity-nesting birds is considered to be relatively low compared with cup-nests – but to date no studies have examined effects of parental nest visitation on predation risk in parrots, which is one aim of this study.

We examine parental care behaviour and nesting outcome at nest cavities of the eastern Regent Parrot (Polytelis anthopeplus subspecies monarchoides). Little is known about its behavioural ecology. The aim of this study is to quantify parental care behaviour at nest cavities and to identify (1) patterns of parental care behaviour during nesting, (2) patterns of nesting outcome (fledged, abandoned, usurped, depredated), (3) effects of nest site attributes (e.g. canopy cover, height, cavity size, distance to water) on nesting outcome, and (4) effects of parental care behaviour on nesting outcome.

**Methods**

**Study site and study species**

The study was conducted at three sites along the river Murray in South Australia, one at Schiller’s Lagoon (adjacent to Lock 2) and two at Hogwash Bend (near Cadell) (Figure 1). Nest observations were undertaken during the breeding season in 2012, 2016 and 2017 from August to November (Baker-Gabb & Hurley, 2011). Male and female Regent Parrots were observed at their nest cavities with the aid of video recordings in 2012, 2016 and 2017, as well as using direct field observations at nest cavities in 2017.

The eastern Regent Parrot (Polytelis anthopeplus monarchoides) occurs in inland south-eastern Australia (Watson, Watson, Luck, & Spooner, 2014) in a single population in the lower Murray-Darling Basin of South Australia, New South Wales and Victoria. It inhabits forests and Mallee woodland (Baker-Gabb & Hurley, 2011). It has declined in both range and abundance and is listed as Vulnerable under the South Australian National Parks and Wildlife Act 1972, Threatened under the Victorian Flora and Fauna Guarantee Act 1988, and Endangered under the NSW Threatened Species Conservation Act 1995 (Sarker et al., 2014; Watson et al., 2014). Current estimates of the population size range from 1500 to 3000 adults.

Regent Parrots depend on eucalypt forests for breeding and nest in cavity bearing trees that are mostly restricted to riparian areas (Krebs, 1998; Watson et al., 2014). They are obligate cavity nesters that always use existing cavities. They are sometimes described as “suppressed colonial nesters”; while they may form colonies if there are sufficient cavities, they may also nest as a solitary pair (R. Webster unpublished data; Eberhard, 2002; Smith, 1992, 2001, 2004, 2006, 2011, Ward & Zahavi, 1973). The
Regent Parrot is socially monogamous and both sexes care for dependent offspring (Krebs, 1998). The incubation duration is ~3 weeks (week 1–3) and the feeding period is ~7 weeks (week 4–10 of the nesting phase, or alternatively referred to as week 1–7 of the feeding phase). Only the female incubates though she is provisioned by the male and both parents provide food to the nestlings (Baker-Gabb & Hurley, 2011). In this study, we did not analyse gender differences in provisioning rates, because we could not distinguish the sexes on our low quality video. Here we analyse overall patterns of nest attendance and time at the nest cavity entrance of the breeding pair.

**Nest cavity observation – video**

Video-recorders were placed at active nests and recorded from dusk to dawn for 10 weeks each. All nests were found at the onset of incubation and hence exposure time was comparable. Twelve unique nest hollows were video-recorded (2012 n = 3 nests; 2016 n = 5 nests; 2017 n = 4 nests). We analysed 608 h of recordings. We sampled six hours of nest behaviour per nest per week across the 10 week nesting phase as follows: 2 x 1 h sampled during the morning (6:00–10:00), 2 x 1 h during mid-day (11:00–14:00), and 2 x 1 h during afternoon (17:00–19:00).

**Nest cavity observation – binoculars**

Three observers (authors EC, TL and SK) observed 13 nests in 2017 using binoculars. The 2017 field nests were unique nests located on the opposite riverbank from the
video-recorded nests in 2012 and 2016. All nests were found at the onset of incubation; continuous behavioural data were collected during the nesting phase due to logistical constraints. In total, 67 h of binocular observations were made during week 3 of feeding and week 5 of feeding, which correspond to week 6 of the nesting phase and week 8 of the nesting phase. During each week of binocular observation, each nest was observed for 2 × 1 h per time of day (morning, mid-day, afternoon), similar to the methods for video recorded nests.

**Parental care**

For each observation period, we noted nest ID, date, time, location, stage of nest since breeding commenced (week), and parental care behaviour. We used the focal sampling method to score parental care behaviour at each nest cavity per hour of observation. The variables analysed in this study include (1) time inside the nest cavity, (2) number of nest visits and (3) time at nest cavity entrance (within 0–3 m of entrance).

**Nesting outcome**

Nesting outcome was assessed for video-recorded and binocular observed nests. Nine nests were video-recorded for 10 weeks (weeks 1–10); three nests were video-recorded for 7 weeks (weeks 4–10); and 13 nests were observed with binoculars up to week 8. The nesting outcome was scored as (1) fledged, (2) abandoned, (3) usurped by another species, (4) depredated, or (5) unknown.

Nests were regarded as having “fledged” if a nestling was observed leaving a nest cavity. Nests were regarded as “abandoned” when both parents did not return to the nest for 2 × 2 h of observation before week 9 or when dead nestlings were found. Nests were regarded as “usurped” if a nest originally used by Regent Parrot for incubation and/or feeding was used by another species in 2 × 2 h observation periods. Nests were regarded as “depredated” when predators were observed at or entering the nest cavity and the nest was subsequently abandoned.

At binocular-observed nests, nesting outcome was assessed from observations during week 3 and week 5 of the feeding phase (week 6 and week 8 of the nesting phase). Nests were regarded as “fledged” if parents were still visiting the nest in week 8; “abandoned” if parents were not seen during two days of nest observation; “usurped” if a different species was seen inside the nest during two days of nest observation; “depredated” if a predator was observed, and “unknown” if activity ceased without any further information.

**Nest site variables**

In 2017, we measured nest site variables at 13 active nest cavities that we observed with binoculars and 3 video-recorded nests. For each nest cavity we measured: (1) latitude and longitude from a GPS, (2) height of the nest cavity (m from the ground), (3) height of the tree (m) measured with a laser range-finder, (4) nest cavity orientation (cardinal direction of cavity entrance), (5) nest cavity length (cm, from bottom to top of entrance) measured with a laser range-finder, (6) nest cavity width (cm, from side to side of entrance), (7) tree diameter (cm) at 1 m from the ground, (8) canopy cover
(percentage cover) above the cavity entrance, (9) number of trees > 2 m within 25 × 25 m (625 m²), and (10) distance to river (m). For visual estimation of canopy cover and distance to river, two field researchers (EC, TL) calibrated distance estimates on different days using a laser distance measurer.

**Statistical analysis**

Statistical analyses were undertaken using SPSS v23. We log10 transformed the three parental care behaviour variables to better satisfy assumptions of normality. Within nests, we used a paired t-test to compare changes in parental care behaviour (time inside nest, number of nest visits, time at nest entrance) from week 1 to week 3 of the incubation phase (n = 4 nests) and from week 1 to week 3 of the feeding phase (n = 14 nests). Between nests, we used an independent samples t-test to compare parental care behaviour at nests observed during incubation (n = 4 nests) versus nests observed during feeding (n = 14 nests). We controlled for time of day by using only data from the morning period. There was a positive relationship between nest length and nest width (r = 0.563, P = 0.036, N = 13), and therefore we used nest length as our estimate of nest cavity size. The environmental variables were highly correlated and we combined them into a set of two uncorrelated Principle Component variables. Using Principle Component Analysis, we extracted two derived factors: PC Size (with high factor loading for tree height, nest cavity distance from ground, nest cavity length) and PC Cover (with high factor loadings for canopy cover, distance to river) (Table 1). We used multiple regression analysis with the two derived factors to test for an association between parental care behaviour and nest site variables. We used MANOVA to test for effects of the ecological variables on nesting outcome (successful versus failed nests). An independent samples t-test was used to compare parental care behaviour in nests that fledged versus nests that failed (abandoned, usurped or depredated) per week of development.

**Results**

**Parental care patterns**

Time spent inside the nest cavity differed across the nesting phase (Table 2). During the incubation phase, parent birds spent 18.5 ± 4.8 min per hour inside the nest cavity and during feeding 10.5 ± 2.9 min inside the nest cavity (t-test: t_{4,14} = 2.272, P = 0.038). The

<table>
<thead>
<tr>
<th>Nest Site Variables</th>
<th>PC Size</th>
<th>PC Canopy Cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest tree height (m)</td>
<td>.874</td>
<td>.015</td>
</tr>
<tr>
<td>Tree diameter (m)</td>
<td>.699</td>
<td>.389</td>
</tr>
<tr>
<td>Cavity height from ground (m)</td>
<td>.874</td>
<td>.092</td>
</tr>
<tr>
<td>Cavity length (cm)</td>
<td>-.723</td>
<td>-.158</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>-.110</td>
<td>.894</td>
</tr>
<tr>
<td>Distance to river (in m)</td>
<td>.530</td>
<td>-.720</td>
</tr>
</tbody>
</table>

**Table 1.** Results of principal components analysis with two derived variables with Eigenvalue greater than 1 that explained 72.3% of the variance. The factor loadings for the two variables are shown below. The two derived variables are referred to as PC size and PC canopy cover.
Table 2. Regent Parrot behaviour (mean ± se) at nest cavities per week of the nesting phase. The data are shown for three time periods across the day (morning, mid-day, afternoon). The behavioural variables are time inside the nest cavity (minutes), number of visits per hour, and time spent at the nest cavity entrance (minutes).

<table>
<thead>
<tr>
<th>Incubation</th>
<th>Morning (06:00–10:00)</th>
<th>Mid-day (11:00–14:00)</th>
<th>Afternoon (17:00–19:00)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inside</td>
<td>Visits</td>
<td>Entrance</td>
</tr>
<tr>
<td>1</td>
<td>7.3 ± 4.49 (n = 4)</td>
<td>0.3 ± 0.2 (n = 4)</td>
<td>1.07 ± 0.79 (n = 4)</td>
</tr>
<tr>
<td>2</td>
<td>14.1 ± 5.62 (n = 4)</td>
<td>0.8 ± 0.3 (n = 4)</td>
<td>0.03 ± 0.02 (n = 4)</td>
</tr>
<tr>
<td>3</td>
<td>18.5 ± 4.75 (n = 4)</td>
<td>0.8 ± 0.3 (n = 4)</td>
<td>0.16 ± 0.11 (n = 4)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Feeding</th>
<th>Morning (06:00–10:00)</th>
<th>Mid-day (11:00–14:00)</th>
<th>Afternoon (17:00–19:00)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inside</td>
<td>Visits</td>
<td>Entrance</td>
</tr>
<tr>
<td>1</td>
<td>17.1 ± 3.55 (n = 8)</td>
<td>2.1 ± 0.4 (n = 8)</td>
<td>0.65 ± 0.28 (n = 8)</td>
</tr>
<tr>
<td>2</td>
<td>17.6 ± 3.91 (n = 8)</td>
<td>2.6 ± 0.8 (n = 8)</td>
<td>1.30 ± 0.54 (n = 8)</td>
</tr>
<tr>
<td>3</td>
<td>10.5 ± 2.88 (n = 20)</td>
<td>1.9 ± 0.3 (n = 20)</td>
<td>3.08 ± 0.87 (n = 20)</td>
</tr>
<tr>
<td>4</td>
<td>14.7 ± 3.01 (n = 8)</td>
<td>2.2 ± 1.1 (n = 8)</td>
<td>2.44 ± 1.42 (n = 8)</td>
</tr>
<tr>
<td>5</td>
<td>4.87 ± 2.03 (n = 20)</td>
<td>2.1 ± 0.4 (n = 20)</td>
<td>2.34 ± 0.60 (n = 20)</td>
</tr>
<tr>
<td>6</td>
<td>4.15 ± 1.79 (n = 7)</td>
<td>1.5 ± 0.5 (n = 7)</td>
<td>1.56 ± 0.73 (n = 7)</td>
</tr>
<tr>
<td>7</td>
<td>4.97 ± 2.17 (n = 8)</td>
<td>1.8 ± 0.7 (n = 8)</td>
<td>1.39 ± 0.54 (n = 8)</td>
</tr>
</tbody>
</table>
number of nest visits differed significantly across the nesting phase: during incubation, there were 0.8 ± 0.3 nest visits per hour and during feeding 1.90 ± 0.30 visits per hour (t-test: $t_{4,14} = 2.810, P = 0.013$). The time at the nest cavity entrance also differed significantly across the nesting phase: during incubation, parents spent 0.2 ± 0.1 min at the entrance and during feeding 3.1 ± 0.9 min at the entrance (t-test: $t_{4,14} = -3.317, P = 0.005$).

Within each nesting phase (incubation, feeding), there were differences in parental care behaviour across weeks. Parental care behaviour at nests during incubation (week 1 versus week 3) at four nests was significantly different for time inside nest cavity ($t = -4.381, P = 0.022$), but did not differ significantly for number of nest visits ($t = -2.274, P = 0.108$) or time at nest cavity entrance ($t = 1.118, P = 0.345$) (Table 2). Regent Parrots spent 86.8% more time inside the nest cavity during week 3 of incubation than during week 1 of incubation (Table 2). Using paired t-tests, the difference in parental care behaviour at nests during feeding (week 1 versus week 3) at 12 nests was significantly different for time inside the nest ($t = 2.213, P = 0.049$), but did not differ significantly for number of visits ($t = -0.471, P = 0.647$) or time at nest cavity entrance ($t = 0.914, P = 0.380$). Birds spent 73.3% less time inside the nest cavity during week 3 of feeding than during week 1 of feeding.

**Nesting outcome**

Of the 25 monitored nests, 13 fledged (52%) and 12 failed (48%) (Table 3). Of nests that failed, 4/12 (~33%) failed during the incubation phase (week 1–3) and 8/12 (~67%) failed during the feeding phase (week 4 to 10). We video-recorded one predation event, where a lace monitor (Varanus varius) climbed a tree trunk, stuck its head inside the hollow and was seen to remove one nestling with which it left the viewing area; this occurred during week 2 of feeding (week 5 of the nesting phase). Six nests were usurped by a different species: 5/6 of Regent Parrot nests were usurped by Yellow Rosella (Platycercus elegans flaveolus) and one by Galah (Cacatua roseicapilla). Four nests were abandoned during the feeding phase and the nestlings died. One binocular-observed nest had an “unknown” outcome; it was active one week and inactive two weeks later.

<table>
<thead>
<tr>
<th>Nesting Outcome</th>
<th>Nest #</th>
<th>Percent of total nests (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fledged Week 9</td>
<td>4, 9, 10, 12, 14, 15, 16, 19, 21</td>
<td>13/25 (52%)</td>
</tr>
<tr>
<td>Week 10</td>
<td>3, 5, 6, 23</td>
<td></td>
</tr>
<tr>
<td>Abandoned Week 6</td>
<td>11, 18</td>
<td>4/25 (16%)</td>
</tr>
<tr>
<td>Week 8</td>
<td>2, 7</td>
<td></td>
</tr>
<tr>
<td>Usurped Week 1</td>
<td>24</td>
<td>6/25 (24%)</td>
</tr>
<tr>
<td>Week 8</td>
<td>8, 22, 25</td>
<td></td>
</tr>
<tr>
<td>Week 3</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Week 6</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Week 8</td>
<td>1</td>
<td>1/25 (4%)</td>
</tr>
<tr>
<td>Depredated Week 5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unknown Week</td>
<td>20</td>
<td>1/25 (4%)</td>
</tr>
<tr>
<td>Week 6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Nesting outcome at 25 Regent Parrot nest cavities. The data are shown for nest cavities that produced fledglings (successful nests) or nests that failed due to abandonment, usurpation, depredation, or unknown cause. The data are shown in relation to week of the nesting phase, with information on Nest ID and the number and percentage of nest cavities per outcome.
Canopy cover differed significantly between nests with different outcomes; nest cavities that produced fledglings had more cover than those that failed (Figure 2, Table 4), whereas no other nest-site variable significantly explained nesting outcome (MANOVA: all $P > 0.05$; Table 4).

**Parental care behaviour and nest site variables**

There was no significant association between parental care behaviour and PC Size (time inside: $r_{\text{part}} = -0.130, P = 0.806$; visits; $r_{\text{part}} = 0.189, P = 0.720$; time at entrance: $r_{\text{part}} = -0.364, P = 0.478$) or PC canopy (time inside: $r_{\text{part}} = 0.357, P = 0.488$; visits; $r_{\text{part}} = -0.030, P = 0.955$; time at entrance: $r_{\text{part}} = -0.067, P = 0.899$).
**Parental care behaviour and nesting outcome**

There were no statistically significant differences in parental care behaviour for any week of development in nests that produced fledglings versus nests that failed (independent t-test, all $P > 0.092$) (Table 5). Nests that were successful did not differ statistically from those that failed in any behavioural variable for any week of comparison. Specifically, we found no difference between the parental birds’ time inside nest (Figure 3), number of visits to the nest cavity (Figure 4), or time at the nest entrance (Figure 5) in relation to nesting outcome.

**Discussion**

Our study on the breeding biology for eastern Regent Parrot (*Polytelis anthopeplus monarchoides*) (1) provides the first quantitative data on average time inside nest, number of visits, and time at entrance across incubation and feeding phase; (2) documents nesting failure whereby 16% were abandoned, 24% usurped, 4% depredated, and 4% unknown; (3) shows that canopy cover of the nesting tree partly explained nesting success; and (4) recorded no effect of parental care behaviour on nesting outcome. This vulnerable subspecies experiences ~50% nesting failure that is a consequence of different processes including interspecific competition for tree cavities, disappearance of adults, and predation by a native reptile. Furthermore, habitat quality appears to be an important factor for nesting success in the Regent Parrot.

As expected, parental care behaviour patterns differed between incubation and feeding stages, which are consistent with changes in development from egg to nestling. Parental care behaviour shifted from spending more time inside the nest cavity (presumably incubating) to more time at the cavity entrance (feeding nestlings). The data in Table 2 provide an overview of average duration and frequency of parental care behaviours for each week of the nesting phase, with the view to informing future field monitoring activity. For example, given that the number of nest visits ranged from 0.3 to 0.8 per hr during incubation and 0.7 to 2.8 per hr during feeding, one would need to observe a nest for at least two hours to estimate activity levels. In other parrot species in Central and South America, the number of nest visits ranged from 0.4 to 3.5 during incubation and 1.8 to 3.4 during feeding (Koenig, 2001; Renton & Salinas-Melgoza, 1999; Waltman & Beissinger, 1992), which is comparable to the results of this study. There was no significant effect of the measured parental care behaviours on nesting outcome. Confirmed nest predation was low (4% of 25 nests), and therefore we could not statistically explore the impact of parental care behaviour on predation. This finding is consistent with the expectation of low predation in cavity-nesting species (Adamík & Král, 2008; Martin & Li, 1992; Rivera, Politi, Bucher, & Pidgeon, 2014), but is lower than recorded in other parrot studies, which report 16–55% nest predation (Koenig et al., 2007; White Collazo, & Vilella, 2005). Another difference between this study and other parrot research is that a lower proportion of Regent Parrot nests failed during incubation ($n = 4; 33\%$) while a higher proportion failed during the feeding period ($n = 8; 67\%$). In other parrot species, failure is reported during incubation; for example Blue-Throated Macaw (*Ara glaucogularis*) (Berkunsky et al., 2014), Tucuman Parrots (*Amazona tucumana*) (Rivera et al., 2014) and Seychelles Black Parrot (*Coracopsis barklyi*) (Reuleaux et al., 2014). The only video-recorded evidence of
Table 5. Summary data for Regent Parrot behaviour (mean ± se per hour) at nest cavities that produced fledglings versus nest cavities that failed due to abandonment, usurpation, depredation, or unknown cause. We only analysed data from 06:00 to 10:00 to control for time of day. The behavioural variables are minutes inside the nest cavity (inside), number of visits per hour (visits), and minutes at the cavity entrance (entrance).

<table>
<thead>
<tr>
<th>Phase/Week</th>
<th>Inside</th>
<th>Visits</th>
<th>Entrance</th>
<th>Inside</th>
<th>Visits</th>
<th>Entrance</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Incubation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>9.8 ± 5.3 (n = 3)</td>
<td>0.3 ± 0.2 (n = 3)</td>
<td>1.4 ± 0.2 (n = 3)</td>
<td>0.0 (n = 1)</td>
<td>0.0 (n = 1)</td>
<td>0.0 (n = 1)</td>
</tr>
<tr>
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<td>0.8 (n = 1)</td>
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<td>1.0 (n = 1)</td>
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<tr>
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<td>7</td>
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Predation in our study was at one nest, by a lace monitor, during week two of feeding. In other Neotropical parrot species, the main nest predators are Boa snakes (Boidae) and boa abundance is thought to explain ~40% nest failure (Berkunsky et al., 2016; Britt, García Anleu, & Desmond, 2014; Koenig et al., 2007). A study on Turquoise Parrot (Neophema pulchella) in north-east Victoria, Australia also found evidence of

**Figure 3.** The average time inside the nest cavity (during the morning from 06:00 to 10:00) (log-transformed data) of successful and failed Regent Parrot nests across each week of the breeding cycle.

**Figure 4.** The average number of nest visits (during the morning from 06:00 to 10:00) (log-transformed data) of successful and failed Regent Parrot nests across each week of the breeding cycle.
reptile nest predation (Quin & Baker-Gabb, 1993). More long-term video recording of nests would be useful to identify nest predators, which are notoriously tricky to detect as predation events vary unpredictably in space and time.

Nest usurpation accounted for 24% of nesting failure and occurred during both incubation and the feeding phase (Table 3). Nest usurpation is a common threat for parrots and may be caused by conspecifics or heterospecifics (Fernandes Seixas & Mourão, 2002; Heinsohn, Murphy, & Legge, 2003; Ortiz-Catedral & Brunton, 2009). Mechanisms that could be driving nest usurpation include interference competition or exploitation competition (Charter, Izhaki, Mocha, & Kark, 2016). In our study, all six usurped nests had evidence of interference behaviour from other endemic parrot species. The nest cavities were visited by the intruders who then occupied the cavity after evicting the eastern Regent Parrot (Lewis, Cantor, Louter, & Kleindorfer, in press), which suggests that nest cavities could be a limiting resource. Habitat features such as the number of old or dead trees with cavities can influence the number and types of nests that are usurped. It is known that within habitats with fewer cavities and little heterogeneity, there is greater competition for cavities (Lindell, 1996). The limited availability of cavities for secondary cavity nesters commonly results in competition between cavity-nesting species using similar sized cavities (Charter et al., 2016; Selman, Perrin, & Hunter, 2004). In Australia competition for cavities can be intense because many species (~300) depend on them (Grarock, Lindenmayer, Wood, & Tidemann, 2013). Furthermore, cavity development is reliant on the slow process of decay in trees as no Australian animals excavate cavities. Despite the importance of cavity nests for reproduction in Australian birds, most research into competition among cavity-nesting species comes from the northern hemisphere (Grarock et al., 2013). With limited information about usurpation in parrot species, much remains to be learned about the biological impact of various patterns of nesting outcome in the eastern Regent

**Figure 5.** The average time at the nest cavity entrance (during the morning from 06:00 to 10:00) (log-transformed data) of successful and failed Regent Parrot nests across each week of the breeding cycle.
Parrot and determining the presence and extent of nest cavity limitation for eastern Regent Parrots might be useful for future conservation management.

Nest abandonment accounted for 16% of nests (Table 3). While most abandonment was during the nesting phase, the sample size was too small to draw conclusions. Generally in other studies, and as expected if nests are observed from nest initiation onwards, nest abandonment commonly occurred during incubation (Traylor, Alisauskas, & Kehoe, 2004; Berkunsky et al., 2016; Sanz & Rodriguez-Ferraro, 2006). In other parrot species, nest abandonment was 10% in Burrowing Parrot (Cyanoliseus patagonus) (Masello & Quillfeldt, 2002), 12% in Tucuman Parrots (Amazona tucumana) (Rivera et al., 2014) and 22% in Green-rumped Parrotlet (Forpus passerinus) (Waltman & Beissinger, 1992). Nest abandonment has been shown to occur as the result of harassment, inclement weather, food scarcity or disappearance of one parent (Rivera et al., 2014; Waltman & Beissinger, 1992). One case of abandonment in the eastern Regent Parrot was associated with parental absence from the nest. At one nest, the male failed to return to the nest during week 5 of feeding and subsequently the nest was abandoned by the female. The male absence could have been due to mortality, perhaps from disease, human persecution, or a road side fatality. Given that Regent Parrots travel on average 5 km to food sources, there are a range of possible fates associated with long-distance foraging (Baker-Gabb & Hurley, 2011). From a separate study, we know that Noisy Miner (Manorina melanocephala), an endemic hyper-aggressive honey-eater, were most active at Regent Parrot nests during the feeding phase, and they may have had a negative effect on nesting success by altering parental time budgets to defend the nest hollow or foraging sites (Lewis et al., in press). Clearly, given the vulnerable status of Regent Parrot, understanding the causes of abandonment should be a research priority.

Regent Parrot nests that produced fledglings had ~58% tree canopy cover compared with ~34% canopy cover at nests that failed. Current research regarding the influence of ecological characteristics on nest cavity success is highly variable between studies (Kozma & Kroll, 2010). Some studies have found that cavity height (Berkunsky et al., 2016; Evans et al., 2002), cavity morphology (Berkunsky et al., 2016; Bourgeois & Vidal, 2007) or canopy cover (Deng & Liu, 2015) affected nest success, while others found no effect of ecological variables on nesting success (Brightsmith, 2005; Stojanovic et al., 2017). Some parrots have an ecological preference for mature forest. For example, the Red-browed Amazon (Amazona rhodocorytha) and Orange-winged Amazon (Amazona amazonica) nest in larger trees. Blue-chested Parakeet (Pyrrhura cruentata) nest in cavities with greater canopy cover (Marsden, Whiffin, Sadgrove, & Guimaraes, 2000), and Red-rumped Parrot (Psephotus haematotus) (Lowry & Lill, 2008) and Lilac-crowned Parrot (Amazona finschi) (Monterrubio-Rico, Ortega-Rodriguez, Marín-Togo, Salinas-Melgoza, & Renton, 2009) nest in areas with tall trees with dense canopy cover. The fitness benefits of nesting in areas with tall mature trees with dense canopy cover could be increased concealment from predators (Deng & Liu, 2015; Griesser & Nystrans, 2009; Lima & Dill, 1990), nest usurpers, or brood parasites (Moskát & Honza, 2000; Vogl, Taborsky, Taborsky, Teuschl, & Honza, 2002). It is likely that habitat quality is an important variable for nest success in the Regent Parrot breeding habitat (Figure 1).

This study into the ecological context of parental care behaviour and nesting outcome in the eastern Regent Parrot revealed important patterns. On the one hand, parental care behaviour did not appear to determine nesting outcome, yet the data
provide useful baseline information to inform monitoring programs. On the other hand, nest site variables exerted some influence on nest success rate. In particular, canopy cover was associated with nesting outcome. Given evidence for nest harassment, nest usurpation and nest abandonment that could be impacted by nest detectability, conservation management approaches could focus on habitat improvement that sustains quality nest sites for this vulnerable species.

Acknowledgments

We thank the Regent Parrot Recovery Team for logistical support, assistance with field work, and for collecting and providing the video-recordings that we analysed here. Thank you also to R. Schmitke for field assistance and discussion about Regent Parrot behaviour. We thank the Department for Environment and Water (DEW) in South Australia for access to resources and information about Regent Parrot nesting behaviour. We thank M. Lethbridge for discussion and support with mapping nest sites. We thank J. O’Connor for advice on developing the video-recording system.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The 2017 field work using binocular observations was funded by Flinders University College of Science and Engineering. The project was approved by the Flinders University Animal Welfare Committee (E458).

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References


