Australian Field Ornithology 2018, **35**, 1–7
http://dx.doi.org/10.20938/afo35001007

Interactions between Australian Ravens and raptors in a pastoral area of New South Wales: Interspecific aggression and nest-site spacing

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Abstract. This study, near Tamworth, New South Wales, investigated the interactions within a diurnal raptor and Australian Raven *Corvus coronoides* community. The Australian Raven (hereafter 'Raven') is an abundant breeding resident here, is the only corvid that breeds in the area, and is known to have a close association with many raptor species. It is known to interfere with nests, provide frequent harassment and decrease the breeding productivity of several nesting raptor species, yet few studies have been completed on this issue, and its significance remains unknown. The abundance of raptors and Ravens and diversity of raptor species were determined from weekly surveys along a fixed 60-km transect in autumn to late spring 2016. A negative association was found between raptor species diversity and Raven abundance. The density and distribution of active or potential raptor and Raven nests were also recorded along the transect: active raptor nests had significantly more active stick nests of other species (raptors and Ravens) nearby (within 500 m), whereas active Raven nests had fewer such active nests within 500 m. Intruding Ravens and Wedge-tailed Eagles *Aquila audax* elicited significantly higher rates of defensive interactions from nesting Black Falcons *Falco subniger* than did other diurnal raptor species; Ravens triggered the highest rate of response. An increased understanding of the factors responsible for shaping community structure is useful for the management of threatened species. The raptor assemblage around Tamworth includes five threatened species, at least four of which are known to breed there, making competition for nest-sites here worthy of research.

Introduction

Many different factors capable of influencing community structure have been identified. For avian assemblages, these include resource availability (Thirgood *et al.* 2003; Krüger 2004; McDonald *et al*. 2004; Carrete *et al.* 2005), interspecific interactions (Jaksić 1982; Hakkarainen & Korpimäki 1996; Thirgood *et al.* 2003; Krüger 2004; Sergio *et al.* 2004; Martínez *et al.* 2008), and anthropogenic factors (Brambilla *et al.* 2004; Krüger 2004). Competition is thought to play an important role in raptor-community structure, as raptors are highly territorial, and competitive interactions (harassment, aggressive exclusion, kleptoparasitism and predation) are needed to establish, defend and maintain territories (Jaksić & Braker 1983; Brambilla *et al.* 2004; Martínez *et al.* 2008; Jiménez-Franco *et al.* 2011). Understanding factors that shape community composition can assist ecologists in conservation management for vulnerable species (Oro *et al.* 2009; Sarà *et al.* 2016). In raptor communities, for example, Sarà *et al.* (2016) modelled competitive interactions (nest-site use by Peregrine Falcons *Falco peregrinus* and Lanner Falcons *F. biarmicus*) to predict nest occupancy by the threatened Lanner Falcon.

Ravens *Corvus* spp. and raptors are frequently found in close proximity, they often share similar habitat, compete for food or overlap in diet, and some raptors (especially falcons *Falco* spp.) depend on ravens for nest-sites (Marchant & Higgins 1993; Higgins *et al.* 2006). There is an agonistic relationship between falcons and corvids, including interference interactions such as nest destruction, harassment, and predation on chicks and eggs by corvids (e.g. Potapov & Sale 2005; Ratcliffe 2010; Debus & Tsang 2011). Conversely, large falcons sometimes prey on or kill ravens (Olsen *et al.* 2004; Potapov & Sale 2005; Debus & Tsang 2011). Although there is much anecdotal evidence, this relationship between raptors and ravens has rarely been tested quantitatively.

This project investigated the factors influencing the structure of an Australian diurnal raptor community in a semi-arid, agricultural region of Australia. The raptor assemblage in this area includes five species that are listed as threatened under the New South Wales *Threatened Species Conservation Act 1995*: Square-tailed Kite *Lophoictinia isura*, Little Eagle *Hieraaetus morphnoides*, Spotted Harrier *Circus assimilis*, White-bellied Sea-Eagle *Haliaeetus leucogaster* and Black Falcon *Falco subniger*, the last four of which are known to breed in the vicinity (this study; S. Debus pers. comm.). In particular, this study focused on interactions between the Australian Raven *Corvus coronoides* (the only corvid known to breed in the area; hereafter 'Raven') and diurnal raptors, as part of a broader study on the breeding ecology of the Black Falcon (Debus *et al.* 2017a,b). The study site supports abundant resident populations of Ravens, with numbers known to increase during lambing, sowing and harvesting times (Rowley 1973), events which usually coincide with the raptor breeding period of typically late winter to late spring in southern Australia (Debus 2012). Previous studies in the region have reported aggression between this corvid and a threatened raptor species (the Black Falcon), whereby harassment and egg predation by the Raven caused breeding failure for this vulnerable raptor (Debus & Tsang 2011; Charley *et al.* 2014).

If competition were present between ravens and raptors generally, we hypothesise a negative association between raven abundance and the diversity and abundance of raptors. A common form of assessing competition in raptor assemblages is by measuring the distance between inter- and intraspecific nest-sites (Solonen 1993; Hakkarainen *et al.* 2004; Martínez *et al.* 2008). The distance between nests is known to increase as a consequence of increasing competition. It is presumed that those species with greater interspecific nest distances are capable of exerting greater territorial defence over other species, and those with smaller distances to nearby nests are thought to exert less competitive pressure.

In comparison with the extensive research on overseas raptor communities, little has been done in Australia (Baker-Gabb 1984a,b; Falkenberg *et al.* 2000; Aumann 2001a–d; Olsen *et al.* 2006; Corbett *et al.* 2014; Aumann *et al.* 2016), and these studies have focused on raptor diet and breeding biology, with few addressing competitive interactions [Baker-Gabb 1984b (including ravens); Aumann 2001a–d]. This study aimed to broaden knowledge in this area, in a community containing several threatened raptor species.

Study area and methods

Study area

The study area was farmland in the sheep–wheat belt of northern inland New South Wales near Tamworth (31°5′S, 150°55′E) (Figure 1). The landscape was mostly cleared sheep and cropping (barley, wheat and canola) farmland, and several tributaries of the Peel River crossed the transect route. The study site, in Australia's semi-arid zone, receives on average 100–200 mm and 200–300 mm rainfall in winter and summer respectively (Bureau of Meteorology 2016).

The Australian Raven is the only corvid that breeds in the Tamworth area. Interactions between this species and raptors were investigated by recording the abundance and diversity of the diurnal raptor and Raven community, and quantifying aggressive or defensive interactions between Black Falcons, Ravens and other raptors. Using methods similar to other studies, inter-nest distances were used to assess the degree of interaction and possible competition.

Raven and diurnal raptor abundance and raptor diversity

A 60-km transect was driven almost weekly around the study area. This was driven in the same direction at ~50 km per hour, starting at 0900 h and lasting *c.* 1.5–2 h, allowing for stops to identify distant raptors, record behaviour and record GPS waypoints of nests. It was driven once every second week between 14 May and 1 July 2016, and then twice weekly from 2 July to 12 November, when breeding activity of Australian Ravens and raptors increased. The total number of surveys completed was 28. For each survey, the weather was recorded as either: Good (wind speed <15 km/h, ambient temperature >10°C, no rainfall; *n*=5), Medium (wind 15–39 km/h, temperature <10°C, <15 mm rainfall in that 24 h; *n* = 5), or Extreme (wind >39 km/h, temperature <0°C, >15 mm rainfall; *n* = 18). Wind speeds and temperatures are values taken from the start of the survey (0900 h), but rainfall is the total for the day (24 h). Surveys were not completed during rainfall or after periods of prolonged rainfall (3–7 days of >8 mm rain each day), as roads became flooded and impassable. In this scenario, surveys were either completed at the next possible date, or went uncompleted for that timeslot (*n* = 6). Sometimes

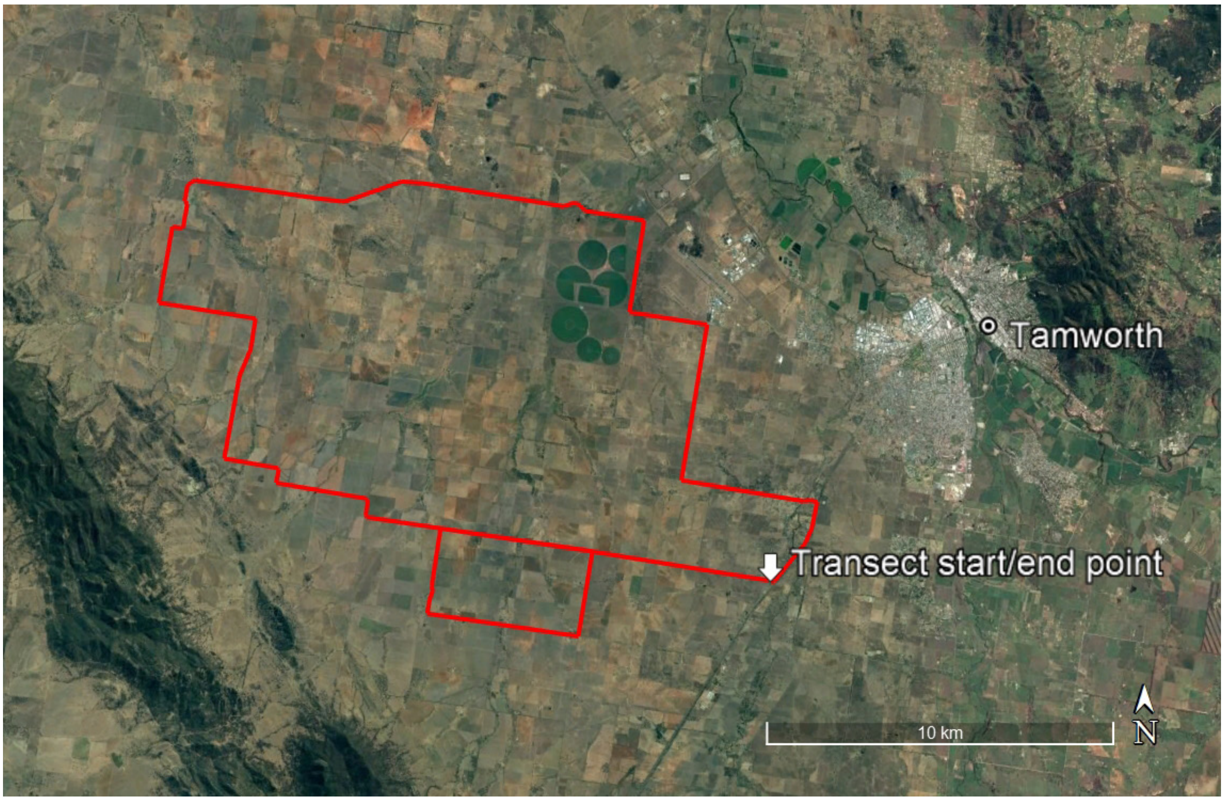

Figure 1. Map of the 60-km transect route along backroads in the Peel Valley region of northern inland New South Wales. The transect started near Warral, extending north-west to Winton and south-east to Bithramere, finishing at the starting point (these localities are ~20 km west and south-west of Tamworth city).

more than one observer was present during the survey, and this was also recorded on the data sheet.

During the surveys, all diurnal raptors and Australian Ravens sighted were counted, with identity confirmed using binoculars (Nikon Monarch 10 × 42) and a telescope (Kowa TSN-661 spotting scope with 10–60× zoom lens), and behavioural observations and nest locations were recorded. All breeding ravens recorded were the Australian Raven. The occasional non-breeding flock of Little Ravens *C. mellori* in autumn–winter was excluded from calculations, as that species does not breed in the study area and appeared to be simply visiting or moving through the study site.

In order to test for a relationship between raven abundance and raptor diversity, we quantified raptor species richness. The number of different species of diurnal raptor observed on each transect count was quantified using a Shannon Richness Index from the formula recommended by Spellerberg & Fedor (2003). The Shannon Richness Index (H') uses p_i as the proportion of individuals found in species i. The proportion is estimated as $p_i = n_i/N$, where n_i is the number of individuals in species i and N is the total number of individuals in the community. The p_i is then multiplied by the natural logarithm of this proportion (ln p_i). The resulting product is summed across species (S), and multiplied by –1.

$$H' = -\sum_{i=1}^{s} p_i \ \mathrm{In}\, p_i$$

First, we tested to see if raptor and Raven abundance were influenced by two potentially confounding effects: the number of observers (either one or more than one) and the weather during transects (either Good, Medium or Extreme). Linear Mixed Models (LMMs) were used to test the relationship of each effect independently on the dependent variable raptor abundance per survey. LMMs were fitted using the 'lmer' function in the package *lme4* (Bates *et al.* 2015). The relationship of Raven abundance relative to raptor abundance or richness per survey was then tested using a Likelihood Ratio Test (LRT) with an *alpha* level of 0.05 and observer number as a random effect. All statistics were calculated in R version 3.2.2 (R Core Team 2015).

Distribution of Raven and diurnal raptor nests

Data were collected during the regular transects, and by walking through woodland patches to find further nests. When encountered, large stick nests were inspected, using binoculars and a telescope, for breeding activity. Only active, attended stick nests of raven size or larger were included in these surveys, as raptors such as falcons use nests of this size (Marchant & Higgins 1993; Debus 2012). The nests of all diurnal raptor species on the transect were also located in the same manner, or by using behavioural cues such as following birds in flight or investigating nests near perch locations. Nests were considered to be active if courtship behaviour, nest construction, regular attendance or defensive behaviour was observed at the nest or nest-tree. Nests were found in various stages of the breeding cycle, including during incubation or the nestling period, and were monitored almost weekly. Unattended nests that were still intact (i.e. the floor of the nest had no visible holes because of weathering) were classified as raven nests and were most likely vacated at some stage during the 2016 study period, as raven nests seldom remain fully intact from one season to the next (PGM pers. obs.). All attended raven nests in the survey belonged to Australian Ravens.

To test for relationships (if any) between the distributions of raptor nests and Raven nests (within and between these categories), three categories of sampling points were used: active diurnal raptor nests, active Raven nests, and random locations along the transect. Random locations (distances) along the transect were points selected using a random number generator in Microsoft Excel (n = 13). In each of these three categories, the number of nests of either raptor or Raven origin was recorded within 500 m of the focal point. Differences in the number of nearby nesting species within 1-km sections of the transect were tested for the three aforementioned categories in the Tamworth study area: Raptor nest-sites, Raven nest-sites and Random sites (as the control group).

A two-way Analysis of Variance (ANOVA) test was used to test for a significant interaction (associations/distances) between the types of nests found (Raven versus Raptor) and site type (Raptor nest-site, Raven nest-site or a Random location) on transects. The interaction was removed from the model and the main effects of site type and nest type were then tested for significant differences. A planned Tukey *post hoc* comparison was used to determine the significance of between-group main-effect differences. All statistical analyses were carried out using R version 3.2.2 (R Core Team 2015).

Defensive interactions at Black Falcon nests

Four pairs of nesting Black Falcons were watched from a distance of 80–300 m (mean 155.5 m ± standard deviation 49.2 m, for a total of 268 hours across 118 days), using the optical equipment already described (see Debus *et al.* 2017a for further details). Nests were watched between May and November 2016. All interspecific interactions were recorded. Observations were classified as responses to species that moved within a 300-m radius of the nest area: (1) 'Defensive attacks' where the Falcons made physical contact with or dive-bombed towards the intruder, vocalised, gave territorial flights/displays (see Debus *et al.* 2017a), or flew towards or underneath a high-flying intruding species; or (2) 'No response', when the Falcons demonstrated no obvious behavioural change following a species entering the 300-m zone around nests (for example, no calling or flight towards the individual). Intruding species were grouped into three categories: Australian Ravens, Wedge-tailed Eagles and Other raptors (all other diurnal birds of prey).

Generalised Linear Mixed Models (GLMMs) were used to test for a difference in the proportion of intrusions within 300m of active nests that resulted in a defensive attack from the resident Black Falcons. We used LRTs to see if dropping the fixed factor of intruder species type (Australian Raven, Wedge-tailed Eagle and Other raptors) resulted in a significant reduction in the amount of variance explained by the models. Planned Tukey *post hoc* comparisons were then used to determine significant differences in aggression rates between the three intruding species groups. Statistical analyses were carried out using

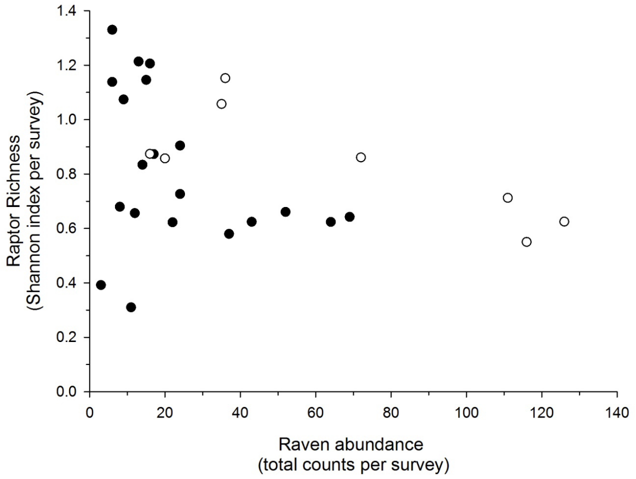

Figure 2. The relationship between Australian Raven abundance and raptor species richness per 60-km survey transect near Tamworth, New South Wales, May–October 2016. Solid circles represent one observer, open circles represent more than one observer per survey.

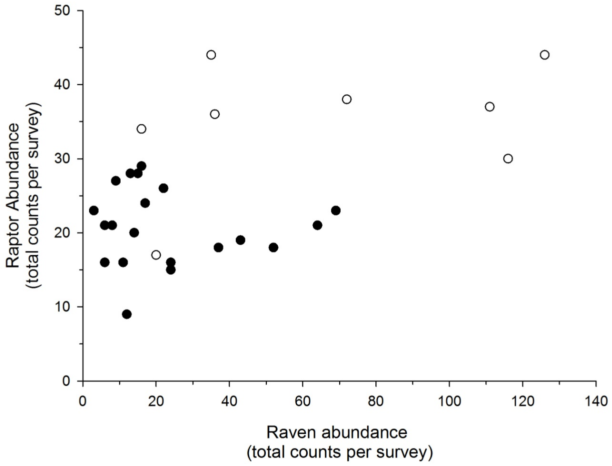

Figure 3. The relationship between the number of Australian Ravens and diurnal raptors observed during the 60-km transect survey near Tamworth, New South Wales, May–October 2016. Solid circles represent one observer, open circles represent more than one observer per survey..

the 'glmer' function in the package *lme4* (Bates *et al.* 2015) using R version 3.2.2 (R Core Team 2015).

Results

Abundance of Ravens and raptors and richness of raptors

Weather type (Good, Medium or Extreme) had no effect on the abundance of birds seen during the surveys ($F_{2,18}$ = 0.768, P = 0.478). However, the number of observers was found to influence the abundance of raptors and Australian Ravens detected ($F_{1, 24}$ = 26.02, P <0.005), meaning that surveys with more than one observer recorded more birds (average 101.4 ± standard error 17.43 total birds per survey) than those conducted with a single observer (average 44.4 ± 4.4 total birds per survey) (Figures 2–3). Multiple observers tended to be present at the time of year when Ravens were moving through the area in larger flocks (~15–30 birds). The number of observers was therefore included as a random variable in further statistical analysis of the transect data to control for this effect.

Although it did not reach statistical significance, the relationship between raptor richness and Australian Raven abundance showed a clear negative trend (χ^2_1 = 3.710, P = 0.0540), raptor species diversity declining with an increasing number of Ravens detected per survey (Figure 2). This result might have been confounded by seasonal effects, e.g. a winter peak in (flocking) Ravens before some raptor species had settled to breed, as well as the multiple-observer effect already noted. There was no significant relationship between the number of Ravens observed on a given transect and the number of raptors seen (χ^2_1 = 1.400, P = 0.237) (Figure 3).

Distribution of nests of Ravens and raptors

Thirteen active nests of diurnal raptors and 90 active Australian Raven nests were located along the transect during the study. On average, 1.5 active Raven nests and <0.25 raptor nest occurred every 1 km of transect. Although there appeared to be an interaction between the type of nests recorded in each of the three categories (Raptor, Raven and Random sites), this did not reach statistical significance ($F_{2, 72}$ = 2.191, P = 0.119). There was a significant main effect of nest-site location, in that significantly more nests were located near Raptor nest-sites, regardless of the nesting species, than both Raven and Randomly selected sites (both Tukey comparisons P <0.005). A trend existed for more nests to be located at Random sites relative to those of Raven nests, but this did not reach statistical significance (P = 0.053). The other main effect in the ANOVA was statistically significant, in that Raven nests were more abundant than raptor nests in the survey ($F_{2, 72}$ = 31.401, P <0.005).

Defensive interactions at Black Falcon nests

A significant difference existed in the proportion of intrusions that led to defensive attacks by Black Falcons according to the type of intruder (χ^2_2 = 23.762, P <0.005). When these results were examined further using *post hoc* analyses, the amount of aggression directed towards Australian Ravens (P <0.005) and Wedge-tailed Eagles (P = 0.018) was significantly greater than that towards other raptor species (Figure 4). The Australian Raven caused the highest rates of interspecific interactions by Black Falcons overall. The proportion of intrusions leading to aggressive defence did not differ significantly between Australian Ravens and Wedge-tailed Eagles (P = 0.312: Figure 4).

Each of the four Black Falcon nest-sites in this study had a pair of Wedge-tailed Eagles nesting nearby (one nest being only 400 m away), and the Eagles were often seen soaring in the vicinity of the Falcon nests. Interactions between these species during the Falcons' incubation period involved flying and displaying or calling underneath the high-soaring Eagle; interactions became more intense in the Falcons' nestling stage, where interactions were often highly aggressive and physical. During this stage, Falcon aggression towards intruding Eagles included strong mobbing of the Eagle, sometimes by both members

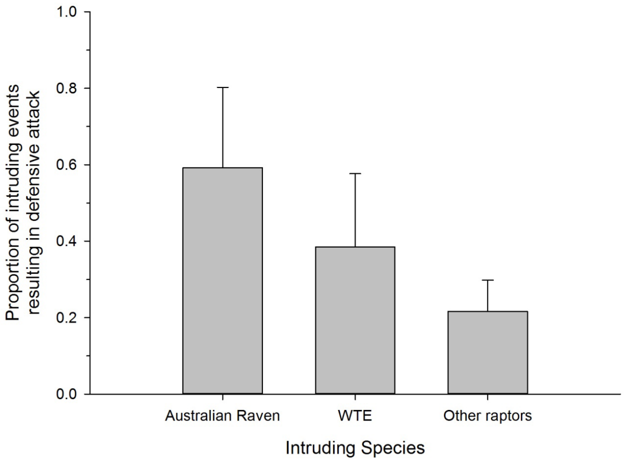

Figure 4. Average proportion of intrusions within 300-m radius of four active Black Falcon nests (Tamworth, New South Wales, May–September 2016) resulting in an aggressive response from the Falcons according to three types of birds: Australian Ravens (*n* = 45), Wedge-tailed Eagles (WTE; *n* = 46) and Other raptors (all other diurnal birds of prey; *n* = 89). Bars indicate means, with error bars indicating 1 standard error.

of the pair working together to mob it by swooping from above, the Eagle often dodging to evade contact (see Debus *et al.* 2017a).

Discussion

This study investigated interspecific interactions between Australian Ravens and the raptor community in a sheep and wheat farming region, where ravens are abundant (Rowley 1969, 1973; Higgins *et al.* 2006), and anecdotal reports have suggested that Ravens are causing nesting failures for one of the threatened raptor species found there (Debus & Tsang 2011). To our knowledge, few studies have quantitatively examined raptor–raven interactions. Studies in Italy on the Peregrine Falcon and Northern Raven *Corvus corax* exhibit disparate results. Brambilla *et al.* (2004) found Peregrine Falcon productivity to be negatively affected by coexistence with Northern Ravens, yet Sergio *et al.* (2004) found productivity to be positively affected. Sergio *et al.* (2004) found Peregrine Falcon productivity to increase with proximity to raven nests, and suggested that ravens might provide an early warning cue and safer nest-sites for nearby Peregrine Falcons. Conversely, Brambilla *et al.* (2004) found that Peregrine Falcons fledged no young at sites where there were ravens as well as frequent human disturbance, because this falcon flushed early when humans were nearby, thus allowing ravens to prey on eggs and chicks at the unguarded nest. Poole & Bromley (1988) investigated ravens and raptors, including the Peregrine Falcon, and found that intra- rather than interspecific relationships were important for nest spacing.

Here, we quantified the number of nearby nests to investigate raptor–raven interactions on a broad community-based scale. The raptor community at Tamworth includes five threatened species, and several species that use Australian Raven nests as their own (Debus 2012; this study). Our results on raptor and Raven nest distribution suggest that raptors and Ravens show opposite behaviour when selecting nest-sites, in that raptors are nesting in areas with more densely packed nests, whereas Ravens tend to nest in areas with fewer nearby nests than randomly chosen sites. Our results suggest that raptors prefer or are confined to choosing areas with higher numbers of nesting Ravens, and Raven nests are significantly more abundant in the area. However, it was not possible to determine whether the raptors at Tamworth might be choosing to nest near Ravens, or are constrained to use these areas (e.g. clusters of vacant Raven nests in riparian areas).

Active Australian Raven nest-sites had a lower number of nearby active Raven nests. This suggests that Ravens appear to be avoiding other Raven nests, a likely explanation for the even distribution of active Raven nest-sites in the study area, where Ravens have a mosaic-like dispersion of territories, agreeing with the literature (Rowley 1973; Higgins *et al.* 2006).

Raptors nest in areas with significantly more nearby raptor and raven nests, in Australian (Baker-Gabb 1984a; Aumann 2001b; M^{c}Donald *et al.* 2003) and overseas raptor assemblages (Gainzarain *et al.* 2000; Sergio *et al.* 2004; Martínez *et al.* 2008; Jiménez-Franco *et al.* 2011; Treinys *et al.* 2011). A study on Central Australian raptors (Aumann 2001b) provided several lines of evidence that stick nests were a limited resource for falcons (though not for nest-building accipitrids): (1) a positive correlation between breeding density and appropriate trees meeting species-specific criteria, (2) an association between density of falcons and availability of stick nests, and (3) the restriction of breeding for many species to narrow riparian woodland belts. Aumann's (2016) study could not determine whether a shortage of stick nests depresses breeding in riparian raptor assemblages; instead, he concluded that a shortage of available stick nests on some creeks would likely delay or prevent some pairs of falcons from breeding during plentiful years. Similarly, at Tamworth, the breeding raptors were mostly aggregated in woodland belts, especially those lining creeks or rivers. Although finer detail was beyond the scope of the present study, it seems likely that the aggregation of breeding raptors is the result of the resource availability in riparian zones, especially considering that the remainder of the study area was mostly cleared land for agriculture and housing.

A link between raptor body size and rates of aggression was evident in this study, where rates of aggression were high between the Black Falcon and Australia's largest raptor, the Wedge-tailed Eagle (Marchant & Higgins 1993; Debus 2012; Olsen 2014). The Wedge-tailed Eagle stimulated more aggressive interference than all other raptor species combined. This result also agrees with previous research, in which the larger species in a raptor assemblage elicit aggression from other species in defence of territories or against potential predators (Temeles 1990; Garcia & Arroyo 2002; Sergio & Hiraldo 2008).

Australian Ravens stimulated an even higher rate of aggression from Black Falcons than that of the larger Wedge-tailed Eagle, a result that suggests a stronger defensive or competitive relationship. An artificially boosted population of Australian Ravens in agricultural areas (Rowley 1973) is thought to increase the level of competition between the two species (Debus 2009, 2015; Debus & Tsang 2011). Competition between these species has been reported anecdotally (Debus & Tsang 2011; Debus & Zuccon 2013; Charley *et al.* 2014). Black Falcons occupy raven nests and even fight with ravens over nests (Debus *et al.* 2017a), and the two species share habitat, overlap somewhat in food resources, and are similar in size (Marchant & Higgins 1993; Debus & Olsen 2010; Debus 2012), key factors in indicating competition (Hardin 1960; Chesson 2000; Hillerislambers *et al.* 2012).

Our study provides a baseline for further research into raptor–raven interactions in semi-arid eastern Australia. Data on the interspecific interactions of focal individuals observed for set time periods when encountered along a survey (cf. Aumann 2001a) would likely provide a greater level of understanding of raptor and raven competition.

Acknowledgements

This study formed part of a University of New England Zoology Honours project by ALB, co-supervised by Dr Stephen Debus and supported by a research grant from BirdLife Australia Northern NSW and the School of Environmental and Rural Sciences, UNE. We thank the landholders for permission to watch the breeding Black Falcons on their land, and Matt and Sarah Berlyn, Greg and Madelon Blaxland and Gavin Hombsch for generously providing field accommodation for ALB. Stephen Debus, Candice Larkin, Nicolas Meyer, Noémie Morel and Josh Osborne participated in some transects and/or nest surveys. This study was conducted under UNE Animal Ethics authority AEC16-02. We thank Stephen Debus, Rohan Bilney and an anonymous referee for comments on drafts of this manuscript.

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Received 29 May 2017, accepted 25 June 2017,
published online 7 February 2018

Appendix 1. Other raptors observed during weekly transects and/or Black Falcon nest watches, additional to Wedge-tailed Eagles and Black Falcons discussed in the text and Figures 2–4. * = observed to be attacked or challenged by breeding Black Falcons during this study.

Black-shouldered Kite *Elanus axillaris*
Square-tailed Kite *Lophoictinia isura*
Pacific Baza *Aviceda subcristata*
*Little Eagle *Hieraaetus morphnoides*
Spotted Harrier *Circus assimilis*
*Brown Goshawk *Accipiter fasciatus*
*Whistling Kite *Haliastur sphenurus*
*Black Kite *Milvus migrans*
Nankeen Kestrel *Falco cenchroides*
Australian Hobby *Falco longipennis*
Brown Falcon *Falco berigora*
*Peregrine Falcon *Falco peregrinus*