Group composition and reproductive success of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*) in urban and non-urban habitat

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Abstract: White-winged choughs (*Corcorax melanorhamphos,* Corcoracidae) are a common, breeding resident in and around the city of Canberra in the Australian Capital Territory. We compared five measures of reproductive success between the urban and non-urban populations of choughs to investigate the effect of urbanization on this cooperatively breeding species. Urban choughs initiated breeding earlier than their non-urban counterparts and were more likely to suffer nest failures. However, there was no difference in the number of successful nests in a season or the number of fledglings produced per successful nesting attempt. A greater proportion of fledglings survived their first 12 months in the non-urban habitat. We suggest that increased rates of nest predation and fledgling mortality in the urban environment may have a negative effect on reproductive success and remove any advantage that might be gained through a longer breeding season. Possible effects of urbanization on the social and genetic structure of white-winged choughs are also discussed.

Key words: *Corcorax melanorhamphos*, dispersal, landscape modification, social behaviour, white-winged chough.

INTRODUCTION

It is becoming increasingly difficult to find landscapes and habitats that are not influenced by human modification in some way. In Australia, 81% of the continental area is actively used by humans (Graetz *et al.* 1995). Therefore, most plants and animals are now living in humanized environments, including cities (Low 2003). However, while the ecology of production landscapes has been well documented through many studies of habitat fragmentation (Barrett *et al.* 1994; Bennett & Ford 1997; Bayne & Hobson 2001), the ecology of urban landscapes has only recently begun to receive attention from researchers. Cities house almost 50% of the global human population and are rapidly expanding (Brown *et al.* 1998). While development and urbanization have overwhelmingly negative consequences for the majority of species, some are thriving in urban environments and it is being increasingly recognized that cities are not wildlife deserts but sustain ecosystems in their own right.

The negative aspects of urbanization are well known and well documented (Major *et al.* 1996; Erritzoe *et al.* 2003; Woods *et al.* 2003). The expansion of urban areas results in the clearing of woodlands, grasslands and other habitat. Cities support greater numbers of introduced species, both feral and domesticated, which are predators or competitors for breeding sites or food supplies, and cities introduce previously unknown hazards such as roads, buildings and airports. However, urban and suburban landscapes also provide a range of advantages to those species that are equipped to exploit them.

For avian species, the primary advantage of the urban environment is the abundance of anthropogenic sources of food and water. Irrigated parks, landscaped gardens, rubbish tips and bird feeders provide reliable and predictable sources of food and water that, unlike many natural sources, are available all year round (Brittingham & Temple 1992; Terman 1997; Bertellotti *et al.* 2001). Consequently, some areas of cities such as suburban gardens are capable of sustaining dense, sedentary populations of species that would otherwise require large territories or migratory behaviour to ensure a sufficient food supply (Noske 1998; Partecke *et al.* 2004). In Britain, it is believed that suburban gardens sustain the highest density of breeding birds of any habitat (Gilbert 1989). Similarly in Brisbane, Australia, Sewell and Catterall (1998) found a higher density of birds in established suburbs with large trees when compared with remnant patches of natural bushland. However, these high densities are usually due to an abundance of a small number of introduced species and generalist native species that have successfully adapted to the

urban environment at the expense of the majority of specialist native species that are dependent on more natural habitat for survival (Catterall *et al.* 1989; Bolger *et al.* 1997; Sewell & Catterall 1998; Lim & Sodhi 2004). Several studies have shown that omnivores, frugivores and opportunistic nectar-feeders adapt better to the urban environment than insectivorous or carnivorous species (Clergeau *et al.* 1998; Lim & Sodhi 2004).

The advantages of urban habitats can also influence breeding behaviour. The warmer temperatures found in cities and the increased food availability may be responsible for the longer breeding seasons observed in urban populations of many species compared with their non-urban counterparts (e.g. Cooper's hawks (*Accipiter cooperii*), Boal and Mannan (1999); rufous-banded honeyeaters (*Conopophila albogularis*), Noske (1998); Australian magpies (*Gymnorhina tibicen*), Rollinson and Jones (2002); European blackbirds (*Turdus merula*, Partecke *et al.* 2005). Wingfield *et al.* (2003) showed that white-crowned sparrows (*Zonotrichia leucophrys oriantha*) exposed to high ambient temperatures had accelerated gonadal development which may lead to an earlier onset of the breeding season. Warmer temperatures may also increase natural food abundance which stimulates reproduction (Svensson 1995).

In Australia, Australian magpies (*G. tibicen*), pied currawongs (*Strepera graculina*) and noisy miners (*Manorina melanocephala*) are examples of native species that have adapted well to the urban environment (Major *et al.* 1996; Rollinson & Jones 2002). In Canberra (population 322 000: Australian Bureau of Statistics 2004), white-winged choughs (*Corcorax melanorhamphos,* Corcoracidae) are also common, breeding residents in older established areas of the urban environment. White-winged choughs are large, ground-foraging, cooperatively breeding birds found throughout the eucalypt woodlands of south-eastern Australia. While still common, there is evidence that the species is declining across its natural range (Barrett *et al.* 2003). Reproductive success in this species is heavily dependent on group size and food resources (Heinsohn 1992). While primarily insectivorous, white-winged choughs are opportunistic foragers that readily take advantage of any available food source including seeds, tubers, bird feeders and rubbish bins. In addition, choughs are mud-nesters and rely on water for nesting material.

Here we present results from the first study of the effect of urbanization on a cooperatively breeding species. We look for evidence for differences in group composition and reproductive success between an urban and non-urban population of white-winged choughs in two breeding seasons following an extreme drought.

METHODS

Study species and site

White-winged choughs are highly social and live year round in groups ranging in size from three to 20. Most groups contain between six and eight members and consist of a monogamous breeding pair and their young from several years. However, newly formed groups may be comprised of unrelated individuals. Choughs are obligate cooperative breeders, pairs have never been observed to breed successfully and even trios rarely succeed (Rowley 1978; Heinsohn 1991). Groups are very cohesive, members travel, feed and roost together and group membership can remain stable for more than 10 years (Rowley 1978). Chough groups do not defend stable territories, but maintain overlapping home ranges of up to 1000 ha in size. Home ranges contract during the breeding season to an area of approximately 20 ha surrounding the nest site. Choughs typically nest from August to January (Rowley 1978). Multiple broods are common and re-nesting occurs quickly after a nest failure.

Nesting attempts of white-winged chough groups were observed in the Australian Capital Territory (ACT) during the 2003/04 and 2004/05 breeding seasons (August to March). Nests were observed in two landscapes: urban areas of Canberra, ACT and a large (1000 ha) nature park on the outskirts of the city. Within the city, chough groups were only found in the older (>40 years), established suburbs of Canberra and nest sites were all located in areas within close proximity to established gardens, parks or nature strips with mature trees. The Canberra Nature Park (CNP), although officially situated within the city of Canberra is an area of dry sclerophyll regenerated bushland dominated by yellow-box (*Eucalyptus melliodora*) and Blakeley's redgum (*Eucalyptus blakelyi*) species. This area does not receive any supplementary food or water from anthropogenic sources; however, it does contain several old farm dams. During the 2 years of this study we saw no movement of groups or individuals between the city and the nature park.

This study occurred following a period of extreme drought which affected most of Australia between March 2002 and February 2003 (Australian Bureau of Meterology 2005). This period was characterized by widespread severe rainfall deficiencies coupled with above average temperatures. Temperatures in the ACT were higher than average during the 2003/04 summer but rainfall was only slightly below average after a winter of above average rainfall. Similarly, the 2004/05 summer was hotter than average but had near average rainfall (Australian Bureau of Meterology 2005).

Field methods

Groups were trapped using large walk-in crow-traps baited with shredded cheese. Once caught, birds were weighed and fitted with individually numbered leg bands from the Australian Bird and Bat Banding Scheme. The age of each bird was determined using the colour of the iris according to Rowley (1975). Age can be determined until birds reach sexual maturity at 4 years. Age was classified as '1' (birds in their first year), '2' (1–2 years), '3' (2–3 years), '4' (3–4 years) and '5+' (birds in their fifth year and older). A small (<50 μL) blood sample was taken from the brachial vein and stored in 70% ethanol for use in genetic analysis. Fledglings were caught by hand within 2 days of leaving the nest.

Nesting behaviour

Surveys in both habitats began in early August to locate nests. Nesting groups were monitored at least three times a week until the last nesting effort was abandoned or successfully fledged. Both the date that active nesting behaviour was first observed and the date that nesting attempts were abandoned or chicks were fledged, were recorded. The fate of each nest was recorded either as 'failed' where a nest was abandoned without producing fledglings, or 'fledged' where at least one chick successfully left the nest. The number of fledglings per nest was also recorded. The stage at which a nest failed was defined as 'eggs', 'small nestlings' (the first 21 days of the nestling period), or 'large nestlings' (the last 7 days of the nestling period). Chough nests are built approximately 10 m off the ground and are extremely difficult to access, making it difficult to determine exactly when the clutch is initiated or at what stage during incubation or brooding a nest fails. Therefore, for successful nests and nests that failed during the 'large nestling' stage we calculated the date that egg laying was initiated as fledging date or failure date minus 48 days (20 days incubation, 28 days nestling period; Rowley 1978). For nests that failed at the egg or 'small nestling stage' we assumed that nests had failed half way through the last stage observed. For example, if a nest had failed at the egg stage, it was assumed that the failure occurred at day 10 of incubation and the date of egg-laying was calculated accordingly. For nests that failed at the small nestling stage, clutch initiation date was estimated as the date of nest failure minus 34 days (20 days incubation, 14 days brooding).

We also investigated differences in the survival of fledglings in the two habitats by recording how many of the fledglings hatched in the 2003/04 breeding season were still alive at the beginning of the 2004/05 breeding season. To do this, we performed a census of fledglings on August 1, 2004. Only banded fledglings from groups that could be located were included in the analysis.

Genetic analysis

White-winged choughs are monomorphic and sex cannot be determined from any visual or frequently observed behavioural cues (Rowley 1978). We determined the sex of each individual using the molecular technique developed by Griffiths et al. (1998) which involves the amplification of a sex-linked chromo-helicase-DNA-binding gene. In addition, all individuals were genotyped at eight polymorphic microsatellite loci (Beck et al. 2003). Pairwise relatedness was estimated following the methods of Lynch and Ritland (1999) and calculated using GenAlEx (Peakall & Smouse 2005). Mean within-group pairwise relatedness was calculated and compared between habitats. We also looked for a correlation between group size and mean pairwise relatedness.

Statistical analysis

All statistical analyses were performed using Genstat 8.1 (VSN International Oxford, UK). We compared five measures of reproductive performance between the city and CNP populations of choughs: the date the first clutch of the season was initiated for each group, the probability of nesting success, the total number of successful nesting attempts in each season, the number of fledglings produced per successful nest and the number of fledglings surviving to the start of the following breeding season. We used a combination of linear mixed models, generalized linear models (GLMs) and generalized linear mixed models (GLMMs) to examine the effect of habitat (CNP, City) and group size on each of these measures. The most parsimonious model was obtained by sequentially removing the non-significant terms until only significant effects remained (Legge 2000). Details of each model are given as follows.

Clutch initiation

For each group, the estimated date the first clutch was initiated each year was recorded as the number of days after July 1. First clutch initiation date was Poisson distributed and normalized with a natural log transformation. We used a linear mixed model including 'Group' and 'Year' as random effects to account for repeated sampling of groups and years. Statistical significance of the explanatory variables and the interaction between them was assessed by Wald statistics when that variable or the interaction term was

included last in the full model. Wald statistics approximate a Chi-square distribution on the respective degrees of freedom.

Probability of nest success

For each nesting attempt, we analysed the probability that nestlings were successfully fledged using a GLMM assuming a binomial distribution with a logit link function (success = 1, failure = 0). Because groups had multiple attempts each year, and some groups were sampled in both years 'Group' and 'Year' were again included as random effects. Statistical significance was tested as above.

Total nest success

For each group, the total number of successful nesting attempts in each season was analysed with a linear mixed model including 'Group' and 'Year' as random effects. Statistical significance was tested using Wald statistics.

Number of fledglings per successful nesting attempt

The number of fledglings produced per successful attempt ranged from one to four in a Poisson distribution and was analysed using a GLMM with a logarithmic link function. Again, as groups and years were sampled more than once, 'Group' and 'Year' were included as random effects. Statistical significance was tested using Wald statistics.

Fledgling survival

The number of 2003 fledglings surviving to 1 August 2004 was analysed using a GLM assuming a Poisson distribution with a logarithmic link function. Each group provided only one response and data were only available for 1 year, therefore there was no need to include 'Group' and 'Year' as random terms. Statistical significance of each variable was tested using deviance ratios that approximate a Chi-square distribution and test the change in deviance when the term of interest is dropped from the full model.

RESULTS

We recorded a total of 112 nesting attempts by 40 different groups and caught 141 fledglings. In 2003/04 we monitored 21 attempts by 14 groups in CNP, catching 32 fledglings, and 37 attempts by 19 groups

in the city, catching 31 fledglings. In 2004/05, we monitored 27 attempts by 18 groups in CNP, catching 45 fledglings, and 27 attempts by 13 groups in the city, catching 33 fledglings. Twelve CNP groups and 12 city groups were sampled in both years.

Group composition

The average group size in the city was 6.5 ± 0.5 SE compared with an average group size of 6.2 ± 0.6 SE in CNP. There was no significant difference in group size between the two habitats (Mann–Whitney U-test: $U = 178$, $P = 0.55$). However, there was a significant difference in the age structure of females between the CNP and city populations (Fig. 1). The mean estimated age of female choughs in the city (3.3 ± 0.19 SE) was significantly lower than that of CNP females (mean estimated age 4.1 ± 0.20 SE; Mann–Whitney U-test: $U = 632.5$, $P = 0.002$). Consequently, there were significantly fewer adult females per group in the city (mean number of adult females per group = 1.2 ± 0.17 SE), than in the CNP (mean = 2.0 ± 0.19 SE; Mann–Whitney U-test: $U = 102$, $P = 0.005$). The sex-ratio of the total population was close to parity (M/F = 0.94) and there was no difference in sex-ratio between the two habitats (CNP M/F = 0.92, City M/F = 0.96).
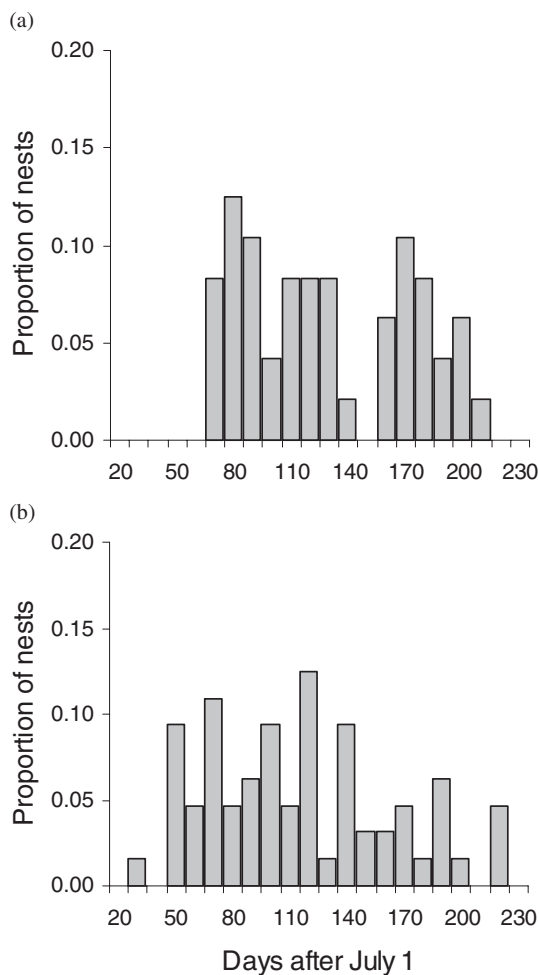
Mean within-group pairwise relatedness was slightly higher in the city ($R = 0.12 \pm 0.01$ SE) than in the CNP ($R = 0.09 \pm 0.02$ SE) but the difference was not significant (two-tailed t-test: $t_{33} = 1.26$, $P = 0.13$). Five groups were newly formed in 2004 and contained individuals that had been members of other groups in 2003. These groups were removed from the analysis so that each individual was included only once in the estimates of mean pairwise relatedness. There was a significant correlation between group size and mean within-group pairwise relatedness in CNP ($R = 0.68$, $P = 0.004$) but not in the city ($R = 0.23$, $P = 0.35$).
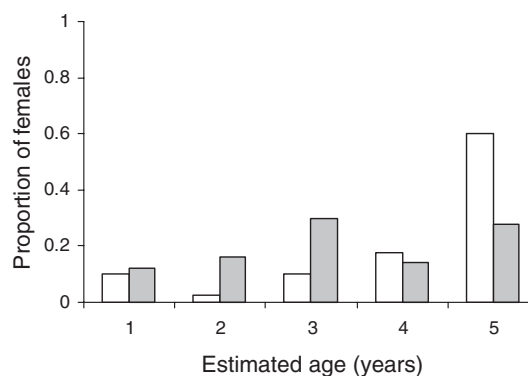
Fig. 1. Age structure of female white-winged choughs in the (☐) Canberra Nature Park and (▨) city populations.

First nests

Figure 2 illustrates the differences in the distribution of all nesting attempts across the breeding season. There was no significant difference in the distribution of nesting attempts between years (Mann–Whitney U-test: $U = 1239$, $P = 0.33$) so data from both years were pooled. The distribution of nesting attempts in CNP was bimodal with the first peak occurring around mid-September (approximately 80 days after July 1) and a second, smaller peak occurring in mid-December (approximately 170 days after July 1). In the city, nesting began in early August (approximately 40 days after July 1) and extended later into January with no obvious modality. Table 1 summarizes the results of the linear mixed model analysis of the initiation of the first clutch in the season. Neither group size nor the interaction between group size and habitat were significant and habitat alone was retained in the most parsimonious model (Table 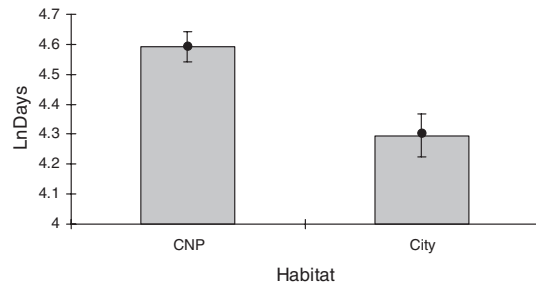1). First clutches were initiated up to 50 days earlier in the city than in CNP. Figure 3 shows the average clutch initiation date for each habitat with the predictions from the best-fitting model.
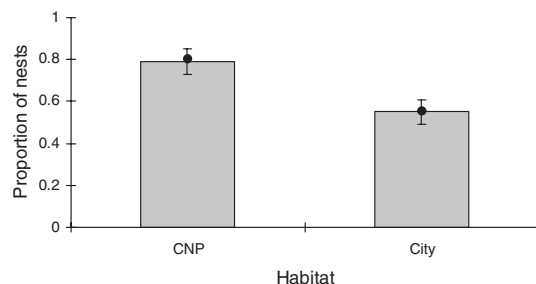
Nesting success

Over the two breeding seasons 79% of nests in CNP successfully fledged young (38/48), while 53% of city nests were successful (34/64). Again, habitat was the only explanatory variable retained in the best-fitting model (Table 1). Figure 4 shows the proportion of nest success in each habitat with predictions from the best-fitting model. However, there was no difference between the habitats in the total number of successful nesting attempts in each season (Table 1; CNP: mean number of successful nests = 1.19 ± 0.11 SE, City: mean number of successful nests = 1.09 ± 0.13 SE).

Number of fledglings

When only successful nesting attempts were considered there was no significant difference between

Fig. 2. The temporal distribution of all nesting attempts of white-winged choughs in both years after 1 July in (a) the Canberra Nature Park and (b) the city.

Fig. 3. Mean date of first clutch initiation in the Canberra Nature Park and the city. Data are represented by bars showing means and standard errors. Predictions from the best fitting model are depicted by solid circles. Average standard error of differences for predictions = 0.092.


Fig. 4. Proportion of nesting attempts that successfully fledged young in the Canberra Nature Park and the city. Data are represented by bars showing means and standard errors. Predictions from the best-fitting model are depicted by solid circles.

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Table 1. Effect of terms in full models for the five measures of reproductive success

Response	Type of model	Random effects	Fixed effects	χ^2	d.f.	P-value
First nests	Linear mixed model	Group Year	Full model			
			Habitat	11.14	1	<0.001
			Group size	2.03	1	0.154
			Habitat × Group size	0.34	1	0.558
Nest success	GLMM	Group Year	Full model			
			Habitat	6.25	1	0.012
			Group size	2.93	1	0.087
			Habitat × Group size	0.05	1	0.830
Total nest success	Linear mixed model	Group Year	Full Model			
			Habitat	0.24	1	0.059
			Group size	3.57	1	0.624
			Habitat × Group size	1.21	1	0.272
No. fledglings	GLMM	Group Year	Full model			
			Habitat	0.01	1	0.924
			Group size	10.00	1	0.002
			Habitat × Group size	0.44	1	0.509
Fledgling survival	GLM	None	Full model			
			Habitat	1.65	1	0.214
			Group size	0.9	1	0.354
			Habitat × Group size	5.21	1	0.035

GLM, generalized linear model; GLMM, generalized linear mixed model.
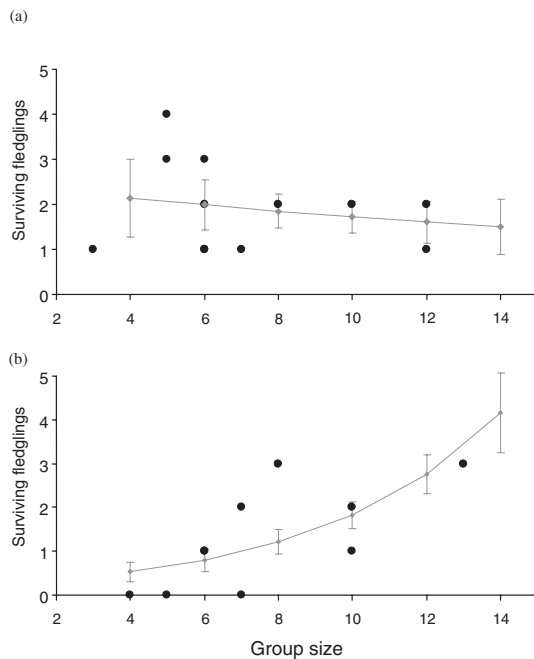
Fig. 5. The number of 2003 fledglings surviving to 1 August 2004 as a function of group size in (a) Canberra Nature Park and (b) the city. Predictions and standard errors from the best-fitting model are shown in grey.

habitats in the number of fledglings produced and only group size was retained in the most parsimonious model (Table 1). Group size had a positive effect on the number of fledglings with larger groups producing more fledglings per nest (data not shown). Mean fledgling weight was slightly higher in the city (240.8 g ± 4.3 SE) than in the CNP (235.4 g ± 2.9 SE) but the difference was not significant (Mann–Whitney U-test: $U = 1290$, $P = 0.066$). Fledgling sex-ratio was slightly female-biased in CNP (M/F = 0.87) but slightly male-biased in the city (M/F = 1.2).

Fledgling survival

In the 22 groups that produced fledglings in 2003 and could be relocated in 2004, 74% of fledglings survived in the CNP and 60% survived in the city. Habitat alone was not significant (Table 1). Instead, there was a significant interaction between habitat and group size. The number of fledglings surviving over the first year increased with group size in the city while fledgling survival in CNP showed a slightly negative effect of group size (Fig. 5).

DISCUSSION

This study found significant differences in both group composition and reproductive success between an urban and non-urban population of cooperatively breeding white-winged choughs.

Reproductive success

Groups of choughs in the city started breeding more than a month earlier than those in CNP. Early initiation of breeding in urban areas has been observed in several species (e.g. Cooper's hawks, *A. cooperii*, Boal & Mannan 1999; Australian magpies, *G. tibicen*, Rollinson & Jones 2002; European blackbirds, *T. merula*, Partecke *et al*. 2005) and could be related to increased food availability, or temperature and photoperiod cues (Svensson 1995; Wingfield *et al*. 2003; Partecke *et al*. 2005). Rollinson and Jones (2002) attributed the early onset of breeding behaviour in suburban Australian magpies to increased food availability through the watering and fertilizing of grassy areas and increased temperatures in suburban areas. White-winged choughs occupy a difficult foraging niche in their natural woodland environment (Heinsohn 1991), but our observations suggest that they are opportunistic foragers in urban areas, taking advantage of anthropogenic sources of food such as rubbish bins and bird feeders. Choughs may also benefit from the increased available water in suburban areas. Choughs are mud-nesters and rely on water for nest building material and in suburban areas are often observed nesting near storm water drains or other permanent sources of water. In CNP most nests are found along creek lines but the population is dependent on rainfall and may start breeding later in years with below average rainfall (Heinsohn 1992).

The breeding season in CNP appears to be synchronous and bimodal, a pattern reinforced by the low levels of nest failure in the CNP. Only 20% of chough nests in the CNP failed during our study and the majority of those could be attributed to a single group whose breeders appeared to be infertile since they failed to hatch a single clutch during the course of this study. In contrast, the lack of modality in the distribution of city nesting attempts across the breeding season reflects the increased likelihood of nest failure followed by rapid re-nesting. The two primary causes of nest failure in white-winged choughs are nestling starvation and predation (Heinsohn 1992). Failures due to starvation usually occur gradually with the youngest nestlings disappearing first, while failures due to predation are more likely to occur suddenly, resulting in the loss of the complete brood. There was no difference between the habitats in the number of fledglings produced per successful nesting attempt but there were many more complete nest failures in the city, suggesting that predation is likely to be the predominant cause of nest failure. Our observations suggest that predation by pied currawongs (*S. graculina*) is likely to be the major cause of nest failures in the urban environment. Pied currawongs are notorious nest predators that take a large range of avian prey (Bayly & Blumstein 2001) and occur at high densities in

Australian urban environments due to the increase of winter food supplied by exotic, ornamental, fruit-producing plants such as privets (*Ligustrum lucidum*) and camphor laurel (*Cinnamomum camphora*; Low 2003). Further work is required to determine the cause of increased nest failures in the city and the extent of currawong predation. However, despite higher rates of nest failure in the city, the total number of successful nests in each season was not significantly different from the CNP, suggesting that city groups continue re-nesting until they are successful.

Group size was the most important factor influencing the number of fledglings produced per successful nest, a result consistent with previous chough studies. White-winged choughs are obligate cooperative breeders. Pairs have never been observed to breed and even trios are rarely successful (Rowley 1978; Heinsohn 1991). Heinsohn (1991) found that the number of fledglings increased linearly with group sizes up to 15 and that only groups of seven or more could raise more than one young on average. Fledgling choughs are poor flyers and are vulnerable to predators. In addition, fledgling survival is related to fledgling weight and food availability over winter. Food supplementation demonstrated that provisioning of chicks is limited by the energetic constraints on the adults (Boland *et al*. 1997) and that post-fledging provisioning will continue into the winter months as long as sufficient food is available (Cullen *et al*. 1996). Heinsohn (1991) demonstrated that fledglings that were partially fed by the group over winter, rather than only foraging for themselves, were heavier and more likely to survive to the beginning of the next breeding season. In addition, fledgling survival was significantly related to group size.

In this study, we found that city fledglings were slightly, but not significantly, heavier but fewer survived over winter. Predation by cats and dogs is likely to occur at higher rates in the city, and juveniles are also more likely to be killed by traffic (pers. obs. 2005; Rollinson & Jones 2002). However, there was a strong relationship between group size and fledgling survival in the city which was not observed in the nature park. We suggest that if the urban environment provides more food over winter then city fledglings are more likely to be fed by the group and less likely to die of starvation than fledglings in the nature park. Where food availability is limited, group size will have less of an effect on fledgling survival. Again, further work is required to test this hypothesis.

Group composition

Habitat had no effect on group size but there was a significant difference in the female age structure between the two populations. The mean estimated age

of city females was lower and there were fewer adult females per group. Changes in the age structure of a population can signal changes in rates of fecundity and survivorship that, in long-lived species, may not yet have translated to declines in population size (Holmes & York 2003). A distribution biased towards juveniles indicates either increased productivity or increased adult mortality or dispersal. We found no evidence for a female-biased fledgling sex-ratio in the city, in fact, fledgling sex-ratio was slightly male-biased. Nor was there any indication of female-biased adult mortality from the small number of band recoveries we have made, although Heinsohn *et al*. (2000) observed female-biased mortality during a period of severe drought. Do adult females, then, disperse more? Avian dispersal is predominantly female-biased (Greenwood 1980) and research suggests that landscape modification that results in increased mortality among dispersers can result in sex-biased populations (Dale 2001) and a younger age structure (Major *et al*. 1999). However, there is no evidence for sex-biased dispersal in white-winged choughs (N. Beck unpubl. data 2005) and no evidence that dispersal occurs more in the urban population than the non-urban population. In fact, dispersal in choughs typically results in small groups with very low mean pairwise relatedness (N. Beck unpubl. data 2005). Therefore, if dispersal was more common in the city population, we would expect lower mean within-group relatedness. Instead, we see slightly higher within-group relatedness in the city. In addition, while relatedness increases with group size in CNP, relatedness is consistently high in the city regardless of group size suggesting lower rates of dispersal.

The results of this study indicate that landscape modification has significant effects on white-winged choughs and suggests several areas for further study. Future research should include determining the proximal causes of the longer breeding season in the city, the increased rates of nest failure and lower fledgling survival. Most interestingly, our results suggest there may be differences in dispersal behaviour between urban and non-urban populations of choughs. Chough dispersal is thought to be associated with periods of severe drought (Heinsohn *et al*. 2000), therefore differences in dispersal behaviour may reflect a degree of 'drought-proofing' offered by the urban environment. An understanding of the effect of urbanization on dispersal behaviour and the consequences for population structure is necessary to appreciate the implications of landscape modification on cooperatively breeding species.

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