

A long-term study of a Western Magpie *Cracticus tibicen dorsalis* population: breeding and productivity

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The widespread Australian Magpie *Cracticus tibicen* exhibits geographical variation in aspects of its sociality and demography. We conducted a 12-year investigation of a colour-banded population of a less well-known subspecies, the Western Magpie *C.t. dorsalis*, to increase understanding of this variation: this report focuses on breeding and productivity. Most female *dorsalis* magpies first bred only when nearly 2 or 3 years old and remained reproductive for 6-12 or more years. As in many other bird species, such delayed reproductive investment may be an adaptive strategy driven by intense competition among population members that have a long breeding lifespan. Nests were mainly built 10-20 m above ground level in eucalypts, providing protection for the young from ground predators. Initiation of females' first clutches of the season peaked from late August to mid-September, the timing resembling that of magpies elsewhere in sub-tropical and temperate Australasia. Nest construction, incubation and nestling brooding were conducted solely by the nesting female and most nestling provisioning was also performed by the apparent mother. However, some females were assisted in feeding their presumed offspring by up to at least two adult males during a breeding season and six males during their monitored breeding lifespan, as well as sometimes by other adult females and immature individuals. Some adult males provisioned the broods of one or two females during a season and of up to five females during their monitored lifespan. Some males provisioned young in up to seven broods produced by a specific female during the study, indicating that in this plural-breeding population there may be long-term associations between specific males and females. Some fledging occurred in nearly half of the broods produced in a season. On average, adult females produced 0.8 fledglings per season and 3+ yearlings in the substantial proportion of their breeding life that was documented. Many features of magpie breeding appear to be widespread (e.g. breeding phenology, preferred nest sites and the exclusively female nest-building, incubation and nestling brooding regimes). The present investigation also showed that adult Western Magpies share features of their offspring care regime with co-operatively breeding magpie populations elsewhere in Australia, but other studies have indicated that they may differ strikingly from such populations in their dispersal and extra-group paternity patterns.

Keywords: Western Magpie; breeding lifespan; timing of breeding; care of offspring; breeding success; productivity

INTRODUCTION

Australian Magpies *Cracticus tibicen* (hereafter 'magpies') are common throughout much of the continent and part of Papua-New Guinea (Menkhorst *et al.* 2017). They were introduced to New Zealand between 1864 and 1900, where they occur as far south as ~46°S (Robertson *et al.* 2007). There are three plumage forms and eight subspecies, hybridization occurring where the various subspecies and plumage forms' ranges overlap (Hughes 1982; Dobson 2017). The most strongly sexually dichromatic sub-species is the Western Magpie *C. t. dorsalis* of south-western Western Australia (Schodde and Mason 1999). Magpies are generalist carnivores, consuming invertebrates and small vertebrates captured at ground level, but also some plant material (Barker and Vestjens 1990). They inhabit open country with low ground cover and scattered trees, and have colonised many conurbations (Rollinson and Jones 2003).

Magpie sociality and demography vary considerably among populations. Throughout their natural and introduced range most magpies defend all-purpose territories year-round (Robinson 1956; Carrick 1963; Veltman 1989; Farabaugh

et al. 1992; Kallioinen *et al.* 1999; Hidayat 2018), but some populations also have non-territorial, non-breeding flocks of 'floaters' that occupy sub-optimal habitat (Hall 1909; Carrick 1972; Veltman 1989; Hughes *et al.* 1996; Durrant and Hughes 2005). In northern Australia, territorial magpies occur mostly in socially monogamous pairs (Farabaugh *et al.* 1992; Hughes *et al.* 1996; Rollinson and Jones 2003) and a proportion of the territorial population also comprises such pairs in some southern populations (e.g. Carrick 1972; Veltman 1989). However, in the southern part of their natural and introduced range territorial magpies mainly occur in groups containing several adults (Robinson 1956; Hughes *et al.* 1996; Veltman 1989; Farabaugh *et al.* 1992; Baker *et al.* 2000; Finn and Hughes 2001), the largest groups occurring in *C. t. dorsalis* populations (Baker *et al.* 2000).

Co-operative breeding (i.e. feeding of nestlings and fledglings by group members other than the likely parents) is negligible in some southern group-living magpie populations (Veltman 1989; Brown and Farabaugh 1991) but common in others (Hughes *et al.* 1996; Finn and Hughes 2001; Pike *et al.* 2019). In some eastern Australian populations, only one female nests at a time in co-

operatively breeding groups containing multiple females (Hughes *et al.*, 1996); in other eastern and western populations plural breeding occurs, in which multiple females nest simultaneously on the same territory (Hughes *et al.* 2003).

Dispersal of many young magpies from the natal territory is common in some south-eastern Australian populations (Durrant and Hughes 2005), typically occurs in the first year of life and appears to be male-biased (Veltman and Carrick 1990; Toon 2007). However, it is negligible in some western populations, which are consequently more genetically distinct than eastern ones (Baker *et al.* 2000), despite extra-group paternity being far more prevalent in some of the western than some of the eastern populations (Hughes *et al.* 2003; Durrant and Hughes 2005). The occurrence of intra-specific brood parasitism has also been inferred from genetic analysis of a Western Magpie population (Hughes *et al.* 2003).

The notable complexity and variability of magpie breeding behaviour revealed by detailed studies of eastern populations during the 1990s (e.g. Farabaugh *et al.* 1992; Hughes *et al.* 1996; Kallioinen *et al.* 1995) motivated us to initiate a long-term investigation of the (then) little-studied Western Magpie in 1996. We felt that a such an investigation could add to the overall understanding of the species' complex and variable ecology, demography and behaviour. The only substantial investigation of *G.t. dorsalis* up to that time had been by Robinson (1956) at Coolup, Western Australia. However, subsequently there have been several further in-depth investigations of various aspects of the behaviour, ecology and genetics of the Perth population that we studied (e.g. Hughes *et al.* 2003; Edwards *et al.* 2015; Ashton *et al.* 2018; Hidayat 2018; Pike *et al.* 2019).

The aim of the present study was therefore to document the breeding behaviour and productivity of a Western Magpie population over several years to facilitate comparison and integration with what is known about these aspects of magpie biology elsewhere in Australasia. Attention was given particularly to the following theoretically important aspects of breeding biology: age at first breeding and breeding lifespan of females, breeding phenology, the features and location of nest sites, the offspring care regime and cooperative breeding, reproductive success and the production of fledglings and yearlings.

METHODS

Study area and population

The 1996-2007 investigation was conducted in an approximately 200 ha area of the Perth suburb of Guildford (-31° 53' 60" S, 115° 58' 22.8" E), which is predominantly a residential area but has sporting facilities, parks and schools, all with extensive grassy areas. Perth's rainfall averages 731 mm annually and falls mainly from May to October, and the mean maximum and minimum daily temperatures between August and December (the main magpie breeding season) are 19.1-29.4°C and 8.4-16.4°C, respectively. The mean number of magpies in the study area at the start of the breeding season over the study period was 89 and annual variation in population size at this time of year ranged only from 79-93 individuals (Rowley *et al.* in prep. a).

Trapping and marking

Magpies were caught in a baited, wire-mesh trap. Trapped birds were weighed (± 1 g) and measured, and their plumage characteristics were recorded in order to age immature birds whose fledging date was unknown (Rowley *et al.* in prep. b). Adult Western Magpies are easily sexed in the field by visual features, the male having a white back and the female black back feathers edged with a white border (Menkhurst *et al.* 2017). Each bird was uniquely marked with stainless steel bands, one being numbered and one to three being coloured. After the initial, intense, broad-scale banding campaign in 1996, the new cohort of juveniles was caught and banded in March-April of each year up to 2005. Population surveys continued until 2007. Few adults immigrated into the population during the study (Rowley *et al.* in prep. a).

Observations

Weekly surveys of most of the population, in which we recorded group size and composition, were conducted year-round. We monitored 12-15 groups per year. During the breeding season, study site visits were made more frequently to locate nests and observe nesting and post-fledging behaviour. We did not conduct extensive time-activity budgeting at nests but regularly recorded which marked birds took the cheese that we proffered to each nest, and we made short (30-80 mins), quantitative observations of provisioning rates of dependent young.

Age at first breeding was determined for a sample of marked female magpies that were caught and banded soon after fledging. All nest trees were identified to species or genus and approximate nest heights were estimated categorically. The timing and duration of breeding stages were determined by observing adults' behaviour, as most nests were too high up to permit direct inspection of contents. We made qualitative observations of breeding behaviour, but also kept systematic records of the sex and identity of all adult birds that fed nestlings and fledglings and the survival of young to independence (~ 2 months post-fledging) and one year of age (assessed in January and September of the year after fledging, respectively). Breeding productivity was estimated in terms of the numbers of fledglings and yearlings produced annually by females and groups.

Data analysis

Relationships among productivity parameters were examined with Pearson's correlation tests (two-tailed). Percentages were arcsine-square root transformed for analysis. Although we used the convention of an α of .05 to assess whether there was significant correlation, we acknowledge the arbitrary nature and limitations of this procedure (Wasserstein *et al.* 2019).

RESULTS

Age at first breeding and breeding lifespan of females

Age at first breeding was determined for 37 marked females; 73% first bred in the second breeding season after hatching when they were nearly 2 years old, 24% when nearly 3 years old and 3% (1 bird) when nearly 4 years old. However, it must be pointed out that failed breeding attempts by some 3 and 4-year old 'debutants' in the year before their first recorded attempt may conceivably have been missed. Success of first breeding

Table 1

Breeding lifespan of marked female magpies at Guildford, 1996-2007. n = number of females. For females which bred in more than one group, the total number of seasons breeding in all groups is given. Unknown start to breeding indicates that breeding probably commenced pre-1996; still present in 2007 indicates that breeding could potentially have continued beyond 2007. Thus, data in columns A, C and D may be incomplete lifetime breeding records because the start and/or end of the breeding lifespan was unknown; data in column B are complete records for the entire breeding lifespan.

Number of breeding seasons	A	B	C	D	n (percent)
	Unknown start, possibly pre-1996; known end pre-2007	Known start in 1996 or later; known end pre-2007	Known start in 1996 or later; still present 2007	Unknown start, possibly pre-1996; still present 2007	
1	6	3	—	—	9 (14.8)
2	3	1	1	—	5 (8.2)
3	3	1	1	—	5 (8.2)
4	4	1	4	—	9 (14.8)
5	1	2	2	—	5 (8.2)
6	—	1	1	—	2 (3.3)
7	2	1	2	—	5 (8.2)
8	—	—	6	—	6 (9.8)
9	—	—	3	—	3 (4.9)
10	—	1	4	—	5 (8.2)
11	—	—	2	—	2 (3.3)
12	—	—	—	5	5 (8.2)
N (females)	19	11	26	5	61

attempts was low, only 32% of first breeders producing at least one fledgling and only 14% at least one young that survived to at least 1 year old.

The number of breeding seasons in which 61 marked females in the most intensively studied groups made breeding attempts in the study area during the investigation ranged from 1-12 (mean 5.7) (Table 1). However, determining the *entire* breeding lifespan was only possible for 18% of these females, for which the range in number of breeding seasons was 1-10 (mean 4.1) (Column B, Table 1). Overall, 42.6% of the monitored, marked females made breeding attempts in the study area in >6 seasons, and 8.2% bred in Year 1 of the investigation (and possibly earlier), were still present at the start of Year 12, and so may have bred in more than eleven seasons.

Breeding phenology

Laying of the first egg of a female's first clutch of the season (n=266) judged from behaviour occurred from mid-August to early November, with a late August to mid-September peak (Table 2). Females' second clutches (n=65) were initiated from late August to early December, with a late October to late November peak. Only three third clutches were laid during the study, all between late October and late November. Thus, for all first, second and third clutches whose production was monitored, laying occurred from mid-August to early December, with a late August to mid-September peak.

Nest sites and nests

Nests (n=310) were constructed in trees belonging to ten genera (Table 3). Eighty percent of them were in eucalypts (Myrtaceae), particularly Flooded Gum *Eucalyptus rudis*, Sugar Gum *E. cladocalyx* and Marri *Corymbia calophylla*. Nests were usually built in a complex fork in the outer canopy of tall trees

Table 2

Timing of laying of first egg determined from observation of behaviour in 334 clutches in the Guildford study area, 1996-2005. Data are the number (and percentage) of clutches initiated in each 10-day period. The three most common laying periods for first, second and all clutches are indicated in bold font in black, red and brown, respectively. Second and third clutches were laid in re-nesting attempts after earlier success or failure.

Date first egg laid	All clutches	First clutches	Second clutches	Third clutches
11-20 Aug	13 (3.9)	13 (5.8)		
21-30 Aug	51 (15.3)	51 (22.6)		
31 Aug-9 Sep	92 (27.6)	91 (40.3)	1 (1.5)	
10-19 Sep	58 (17.4)	57 (25.2)	1 (1.5)	
20-29 Sep	29 (8.7)	28 (12.4)	1 (1.5)	
30 Sep -9 Oct	16 (4.8)	12 (5.3)	4 (6.2)	
10-19 Oct	19 (5.7)	12 (5.3)	7 (10.8)	
20-29 Oct	13 (3.9)	1 (0.4)	11 (16.9)	1
30 Oct-8 Nov	20 (6.0)	1 (0.4)	19 (29.2)	
9-18 Nov	10 (3.0)		9 (13.9)	1
19-28 Nov	11 (3.3)		10 (15.4)	1
29 Nov-8 Dec	2 (0.6)		2 (3.1)	
Total	334	266	65	3

and comprised a twig platform on which was constructed a cup made of twigs and lined with grass, shredded bark, wool or horse hair. Many nests incorporated fencing wire, synthetic rope, electrical cable or even fishing line, some of these materials probably making nests more conspicuous. Approximate heights above ground level of 309 nests were <10m (8%), 10-20m (82%) and > 20m (10%) and some nests were used in more than one breeding season. Although nests were typically well spaced

Table 3

Tree species and genera in which magpie nests were constructed at Guildford, 1996-2007. N = number of nests.

Tree species or genus	Common name	N = rounded percent (percentage)
<i>Eucalyptus rudis</i>	Flooded Gum	137 (44.2)
<i>Eucalyptus cladocalyx</i>	Sugar Gum	65 (21.0)
<i>Corymbia calophylla</i>	Marri	40 (12.9)
<i>Araucaria heterophylla</i>	Norfolk Pine	20 (6.5)
<i>Lophostemon conferta</i>	Brush Box	17 (5.5)
<i>Ficus sp.</i>	Fig	8 (2.6)
<i>Eucalyptus wandoo</i>	Wandoo	6 (1.9)
<i>Corymbia citriodora</i>	Lemon-scented Gum	4 (1.2)
<i>Eucalyptus spp.</i>	Various eucalypts	5 (1.6)
<i>Erythrina sp.</i>	Coral Tree	2 (0.7)
<i>Brachychiton populneus</i>	Kurrajong	2 (0.7)
<i>Cupressus sp.</i>	Pencil Pine	1 (0.3)
<i>Melaleuca quinquenervia</i>	Broad-leaved Paperbark	2 (0.7)
<i>Cinnamomum camphora</i>	Camphorlaurel	1 (0.3)

apart, some females in groups with multiple females often nested in adjacent trees or even the same tree e.g. in two or more years two or three females in NH group nested simultaneously in the same Norfolk Pine *Araucaria heterophylla* about 10 m apart.

Care of offspring

1. Nest-building and incubation

Only adult females built nests and incubated eggs, although when a female had an association with a specific male group-member he would sometimes visit the nest, occasionally provision her there or perch or forage nearby while she was incubating in what appeared to be primarily guarding behaviour (see also Pike *et al.* 2019). Median incubation period duration was 21 days (n=24).

2. Nestling care

The estimated mean nestling period duration was about 32 days (n= 29 broods). During the first 14 days, the female brooded the nestlings extensively, particularly on cold mornings and during rain, and her foraging recesses from the nest were brief (5-10 min). Males did not brood nestlings.

2.1 The role of adult females in provisioning nestlings

- Most nestling provisioning was done by the nesting female, although she was sometimes assisted by one or more adult male group-members. The predominant role of the nesting female was evident in two ways: (i) some females who nested in several years performed all nestling provisioning without any male assistance in any year (e.g. GYB [FP group] who bred in 5 years, Table 4), and (ii) in 19 observation sessions at the nests of seven females who were each assisted by a single adult male, 84.2% of the sessions were characterised by more female than male nestling provisioning and just three had equal male and female feeding effort (Table 5); collectively, nesting females executed significantly more (67%) of the 159 nestling feedings in these sessions than did assisting males ($P < 0.001$, Binomial test).

- Females that received male assistance in feeding their nestlings had multiple (up to six) adult male assistants during the proportion of their breeding lifespan that we monitored (e.g. BSB [FM group] and PS/YX [PG1 group] each had four male helpers during the study, see Table 4).
- Within a single breeding season, assisted females were helped in feeding their nestlings by up to at least two adult males (e.g. RBY [WS group] was helped by males BPS and BYP in 2006).
- Occasionally adult females fed nestlings other than their own, often after their own breeding attempt had failed (e.g. YY/P and RY/G [FM group] fed nestlings in their presumed mother's [VRG] nest after their own breeding attempts failed, Table 4).

2.2 The role of adult males in provisioning nestlings

- Some young adult males were quite active in feeding nestlings (e.g. YP [PG2 group] provisioned nestlings of females YSS and VVR, Table 4) and some older adult males were also quite active (e.g. RGB [FM group] provisioned nestlings of females BSB, SSS and RGR, Table 4), but other males fed nestlings very little.
- Males that assisted in feeding nestlings helped up to five different females during the portion of their breeding life that we could document (e.g. RYR [FM group] assisted females RGR, SSS, BSB, VRG and YY/P, Table 4).
- Adult males assisted in feeding a particular female's nestlings in up to 7 breeding attempts during the study (e.g. VSB assisting female BBV [GG group], Table 4).
- Within a breeding season, assisting males fed the nestlings of up to at least two females (e.g. YSG [PG1 group]). Males sometimes helped more than one female in parallel; others switched from predominantly helping one female to feed her nestlings to assisting a different female later in the same season.

Table 4

Number (in bold font) and identity of adult males and other individuals that fed nestlings and fledglings of females on fourteen territories at Guildford, 1996-2005. Assisting individuals were adult males unless otherwise specified. The number of breeding attempts in which a bird assisted, where known, is given in parentheses after its identity. Adult females and males given as examples of provisioning patterns during the monitored breeding lifespan in the dot points under *Care of offspring* in the Results section in the text are shown in red and purple font, respectively. Fem = female, a.l. = at least, n.d. = no data obtained, n.o. = no assistance of breeding female in feeding young was observed, – indicates no opportunity for provisioning occurred. IM = immature bird. All gp. indicates that a female's fledglings were fed by all or most group members on the territory, but details not recorded.

Group	Female	No. years observed breeding	Group size	No. nests Total, no. producing a.l. 1 fledgling	Birds that fed at nests (no. nests)	No. and identity of birds that fed fledglings (no. broods)	Comments on assisting individuals and (in <i>italics</i>) summary of adult male involvement
FP	<i>GYB</i>	5	4	10, 4	n.o.	3 BBB (1) SGS (3) YRR (2)	BBB also fed GYB while she incubated
	<i>GSY</i>	4	2	4, 2	1 YRR	1 YRR (2)	
	<i>BV/B</i>	2	3	2, 0	0	0	
							<i>No. of females helped by males in FP group: YRR helped 2, BBB and SGS each helped 1</i>
NH	<i>VYV</i>	10	6-9	14, 7	3 SSY (2) VB/B (1) YYY (1)	3 SSY (3) VB/B (3) RSR (2)	
	<i>RBY</i>	8	6-9	13, 7	1 RSR (6)	1 <i>RSR</i> (5)	
	<i>BSY</i>	6	6-9	8, 1	1 SSY (1)	1 VB/B	
							<i>No. of females helped by males in group NH: SSY, VB/B and RSR each helped 2, YYY helped 1</i>
HC	<i>YBR</i>	4	4-5	5, 3	2 GRG (1) SYS (2)	2 GRG (1) SYS (2)	Male SYS fed female YBR while she was incubating
	<i>BGG</i>	5	4-6	5, 3	1 SYS (1)	n. o.	
	<i>RSV</i>	8	5-7	10, 7	2 SYS (4) YY (2)	2 SYS (3) YY	
	<i>YB/B</i>	1	6	1, 0	–	–	
	<i>VS/B</i>	4	6-7	4, 3	2 YY (3) PV (1)	1 YY (1)	
							<i>No. of females helped by males in HC group: SYS helped 3, YY helped 2, GRG and PV each helped 1</i>
LP	<i>YBY</i>	9	4-5	9, 1	2 RRR (1) GYG (1)	1 RRR (1)	
	<i>SBS</i>	8	4-5	9, 2	n.d.	2 RRR (1) GYG (1)	
	<i>Unb. female</i>	1	5	1, 1	n.d.	n.d.	
							<i>No. of females helped by males in LP group: RRR and GYG each helped 2</i>
FM	<i>RGR</i>	3	10-11	3, 3	1 <i>RYR</i> (1) <i>RGB</i> (1)	3 BRG <i>RYR</i> Fem SSS	
	<i>SSS</i>	7	7-13	6, 2	4 YSR (1) SYG (1) <i>RGB</i> (2) <i>RYR</i> (2)	2 <i>RYR</i> (1) <i>RGB</i> (1)	
	<i>BSB</i>	7	7-13	8, 5	4 <i>RGB</i> (2) <i>RYR</i> (2) BRG (3) YSR (1)	4 <i>RGB</i> (1) <i>RYR</i> (2) BRG (1) Fem RBY	
	<i>BVR</i>	2	6-8	2, 1	1 BRG (2)	1 BRG (2)	

Table 4 (continued)

Group	Female	No. years observed breeding	Group size	No. nests Total, no. a.l. 1 fledgling	Birds that fed at nests (no. nests)	No. and identity of birds that fed fledglings (no. broods)	Comments on assisting individuals and (<i>in italics</i>) summary of adult male involvement
FM	VRG	6	6-13	8, 3	6 RYR (1) BR (2) YSR (1) BRG (1) Fem YY/P (2) Fem RY/G (3)	4 RYR (1) BR (1) Fem YY (2) Fem RY (1)	Females YY and RY were daughters of female VRG
	RBV	2	11-13	2, 0	0	0	
	YY/P	3	6-7	4, 2	3 RYR Fem RY Fem VRG	4 RYR (2) BR Fem RY Fem VRG	
	RBV	2	11-13	2, 0	0	0	
	RY/G	2	6-7	2, 1	2 BR Fem RY	—	
							<i>No. of females helped by males in FM group: RYR helped 5, BRG, YSR, BR and RGB each helped 3, SYG helped 1</i>
							In 2001, RBB's sole fledgling was fed occasionally by 4 immatures fledged in the previous year.
OV	RBB	6	6-8	7, 3	2 GGY (5) BYB (2)	5 GGY (2) PP (IM) YS (IM) BY (IM) BB (IM)	
	SRB	4	6-10	6, 2	2 BYB (4) YGR (1)	1 BYB (2)	
	RBG	2	7-8	2, 1	2 BYB (1) YGR (1)	1 BYB (1)	
							<i>Number of females helped by males in OV group: BYB helped 3, YGR helped 2, GGY helped 1</i>
SM	BRB	10	3-7	11, 4	2 Unid male Fem GY	2 YRY (1) Fem GY (1)	Female GY fed at BRB's nest in 2000 after own nest failed.
	GY	6	4-7	6, 4	2 YRY (1) YR (2)	3 YRY (2) YR (2) Fem PB (1)	Adult Female PB fed GY's fledglings
	RR	1	7	1, 1	2 YR (1) YB (1)	2 YR YB	
							<i>No. of females helped by males in SM group: YRY helped 4, YR helped 2, YB helped 1</i>
WB	GRY	1	5	1, 1	n.o.	n.o.	
	VRB	9	2-7	11, 9	3 YYS (3) BSS (1) YB (2)	3 YYS (2) SRR (1) YB	
WS	RBV	2	3-5	2, 2	3 BPS (2) BY (2) Unb 1 yo male	3 BPS BY Unb 1 yo male	
PG2	YSS	8	3-5	7, 2	2 1 leg male YP	1 1 leg male	
	VVR	8	3-5	13, 4	1 YP (3)	1 YP	
							<i>No. of females helped by males in PG2 group: YP helped 2, One leg helped 1</i>

Table 4 (continued)

Group	Female	No. years observed breeding	Group size	No. nests Total, no. producing a.l. 1 fledgling	Birds that fed at nests (no. nests)	No. and identity of birds that fed fledglings (no. broods)	Comments on assisting individuals and (<i>in italics</i>) summary of adult male involvement
MM	VBR	10	6-11	11, 6	2 RRB (2) Limpy	1 RRB (1) Limpy	
	YGB	10	6-11	15, 13	2 VYY (4) Limpy (1)	5 VYY (4) Limpy (1) YYR (3) Fem VRY (1) Fem GR/Y (1)	
	VRY	8	8-11	12, 4	2 YYR (7) Limpy (1)	2 YYR (3) RRB (1)	
	SGGX	6	8-11	6, 5	2 Limpy RRB	1 Limpy	
	PYYX	5	8-11	6, 1	—	1 RRB	
							<i>No. of females helped by males in MM group: Limpy helped 4, RRB helped 2, VYY and YYR each helped 1</i>
PG1	RYB	4+	7-9	4, 3	2 YSG (1) YYV (1)	1 YYV (1)	YSG also fed incubating female RYB
	YRS	1	9	2, 2	—	—	
	VVR	1	9	1, 1	1 YYV (1)	1 YYV (1)	
	BG/YX	6	4-12	8, 3	3 YSG (2) Fem PS (1) RY	3+ YSG (2) Fem PS (1) All gp (1)	
	PS/YX	6	4-12	7, 3	4 YSG (4) GG/P (1) SR/G (1) RY (1)	All gp.	
	BR/YX	5	5-12	6, 6	3 YSG (3) GG/P (2) RB (1)	6+ YSG (4) Fem BG (1) GG/P (2) RB (1) BS (1) Fem PS (2) All gp.	
							<i>Number of females helped by males in PG1 group: YSG helped 4, YYV, RY and GG/P each helped 2 SR/G and RB each helped 1</i>
HR	GSS	3	9-12	3, 3	n.o.	1 RRY (1)	
	YSY	3	9-12	3, 3	n.o.	n.o.	
	YVR	7	10-13	8, 3	1 SYB (3)	1 SYB (2)	
	BB/G	6	10-12	10, 4	1 RVS (2)	2 RVS (3) GYR (1)	
	BP/BX	1	11	1, 0	n.o.	n.o.	
	BY/GX	2	10	2, 0	n.o.	n.o.	
							<i>Number of females helped by males in HR group: RRY, SYB, RVS and GYR each helped 1</i>
GG	BBV	8	3-12	9, 7	1 VSB (7)	3 VSB (5) unb male 00 unb male 01	
	VRY	2	3	2, 1	n.o.	n.o.	
	BR/PX	4	8-12	6, 4	—	3 YY (2) GR (1) PV (2)	
	GX/RS	2	9-12	2, 0	—	—	
	YGG	3	9-12	4, 2	—	n.o.	
							<i>Number of females helped by males in GG group: VSB, YY, GR, PV, unbanded 00 and unbanded 01 each helped 1</i>

Table 5

Frequency of provisioning nestlings by the nesting female and assisting adult male in observations at seven nests in two breeding seasons. In all observations or observation sequences at each nest, only one adult male fed nestlings. NF = nesting female, M = male, — = zero reading.

Nesting female (Group)	Date	Observation duration (min)	No. feeding visits to nest	
RSV (HC)	06/10/1998	80	NF 3	M SYS 1
YBR (HC)	06/10/1998	80	NF 4	M SYS 1
BBV (GG)			NF	M VSB
	07/10/2000	53	7	7
	11/10/2000	48	4	4
	19/10/2000	57	8	5
	23/10/2000	61	7	4
PS/YX (PG1)			NF	M YSG
	23/10/2002	51	5	3
	29/10/2002	42	2	—
	06/11/2002	53	6	3
	08/11/2002	60	3	1
	16/11/2002	60	4	2
VRY (MM)			NF	M YYR
	04/10/2000	56	3	2
YGB (MM)			NF	M LPY
	04/10/2000	56	10	3
RSV (HC)			NF	MYY
	03/10/2000	63	9	5
	06/10/2000	71	7	—
	08/10/2000	59	8	3
	18/10/2000	48	5	3
	23/10/2000	59	9	4
	02/11/2000	30	2	2
Total	19 observations	1,037 min	106 feeding visits	53

3. Fledgling care

Fledging itself was not observed. Immediately post-fledging, young were left perching in vegetation while the presumed mother foraged and then brought them food. Once juveniles could fly proficiently, they pursued their foraging mother and begged food from her or other adult and immature group-members. Juveniles did not self-feed at all until they were about one month old. They were essentially capable of independently sustaining themselves at about two months post-fledging, but still sometimes begged food from their presumed mother or other adults, sometimes successfully.

3.1 The role of adult females in provisioning fledglings

- Most feeding of fledglings was done by their presumed mother, but some adult male and older immature group-members also contributed in some groups. However, some females sometimes fed their presumed fledglings

very little and instead re-nested, leaving the brood to be provisioned by other group-members (e.g. YGB [MM group], Table 4).

- Females that did feed their fledglings substantially and had some assistance in so doing had up to four adult male helpers during the study (e.g. BR/YX [PG1 group] was assisted by adult males YSG, GG/P, RB and BS, Table 4).
- Within a breeding season, assisted females were helped in feeding their fledglings by up to at least two adult males (e.g. BRPX [GG group] was assisted by males YY and GR in 2005).

3.2 The role of adult males in provisioning fledglings

- Adult males assisted in provisioning the fledglings of up to five females during the part of their breeding life that we could monitor (e.g. RYR [FM group] assisted females RGR, SSS, BSB, VRG and YY/P, Table 4).
- An adult male assisted in feeding the fledglings of a specific female in up to five breeding attempts during the study (e.g. RSR assisting female RBY [NH group], Table 4).

Some adult males were never observed to feed nestlings or fledglings during the entire investigation (e.g. BSR [OV group]). Immature birds were sometimes involved in provisioning nestlings and fledglings; however, we did not obtain a complete, detailed record of the involvement of such birds in this behaviour, so the information on this aspect of helper activity in Table 4 is incomplete.

Breeding success

From 1996 to 2005, 47.7% of 308 monitored breeding attempts produced at least one fledgling. Annual variation in this metric ranged from 27.6 to 81.3% (Table 6). There was considerable annual variation in the percentage of breeding failures that occurred during the various developmental stages, but in the whole study 22.1% of breeding attempts failed during incubation and 27.3% in the first half and 2.9% in the second half of nestling development (Table 6).

On average, clutches initiated later in the season were less likely to produce fledglings ($r_{(9)} = -0.695$, $P < .05$) and more likely than those initiated earlier on to fail during incubation ($r_{(9)} = 0.626$, $P < .05$) but not during nestling development ($r_{(9)} = -0.053$, $P > .05$) (Table 7). The reasons for breeding failure were difficult to ascertain because we could not directly inspect nest contents, although we suspect that cold, wet weather may have been one factor. Three nesting females died from entanglement in fishing line incorporated into the nest and two in road accidents. No nest predation was observed, although potential avian and mammalian nest predators were seen near many nests.

Further breeding attempts by females after failure earlier in the season occurred in all years, but constituted only 15.4% of all attempts made during the study. Additional breeding attempts after successful breeding earlier in the season were even less common, comprising only 6.1% of all attempts. The median interval between the successive breeding attempts of females

Table 6

Annual variation in fledging success and breeding failure in Guildford study area, 1996-2005. Nestling period divided into two approximately 14-day segments.

Years (no. of attempts)	Percent attempts in which at least one young fledged	Percent attempts failed (incubation stage)	Percent attempts failed (first half nestling stage)	Percent attempts failed (second half nestling stage)
1996 (20)	55	25	20	0
1997 (16)	81.3	6.3	12.5	0
1998 (25)	68	20	12	0
1999 (29)	27.6	10.3	62.1	0
2000 (31)	54.8	12.9	32.3	0
2001 (36)	47.2	16.7	36.1	0
2002 (40)	55	30	15	0
2003 (38)	31.6	39.5	29	0
2004 (35)	48.6	11.4	28.6	11.4
2005 (38)	34.2	34.2	18.4	13.2
N (attempts) 308	147	68	84	9

Table 7

Fledging success and breeding failure as a function of clutch initiation time (in 10-day time intervals). Interval 29 Nov-8 Dec excluded from statistical analysis in text as n only 2.

Period of clutch initiation (no. breeding attempts)	Percent attempts in which $\geq$ one young fledged	Percent attempts failed during incubation	Percent attempts failed during first half of nestling period	Percent attempts failed during second half of nestling period
11-20 Aug (12)	41.7	16.7	33.3	8.3
21-30 Aug (47)	63.8	14.9	17.0	4.3
31 Aug-9 Sep (85)	63.5	12.9	22.4	1.2
10-19 Sep (55)	36.4	25.5	34.6	3.6
20 Sep-29 Sep (26)	34.6	11.5	46.2	7.7
30 Sep-9 Oct (15)	46.7	26.7	26.7	0.0
10-19 Oct (16)	50.0	18.8	31.3	0.0
20-29 Oct (12)	41.7	33.3	25.0	0.0
30 Oct-8 Nov (20)	20.0	65.0	15.0	0.0
9-18 Nov (8)	12.5	37.5	37.5	12.5
19-28 Nov (10)	30.0	40.0	30.0	0.0
29 Nov-8 Dec (2)	50.0	0.0	50.0	0.0
N (attempts)	147	68	84	9

who re-nested after breeding failure was 60 days (range 30-100, $n = 53$) and the interval between successive attempts by the few females who re-nested after successful breeding averaged 70-80 days (range 60-100).

Fledging success of second and third breeding attempts of the season was low; only 30% of such attempts (i.e. after both failure and success) produced at least one fledgling. Moreover, in 36.4% of these successful additional attempts the fledged young only survived for about 7 days post-fledging. In the entire investigation only two females raised two broods in a season, from each of which at least one young survived to 1 year of age.

Productivity

1. Females

Females produced a mean of 1.1 clutches annually. On average, a breeding attempt produced 0.69 fledglings and individual females produced 0.84 fledglings per season (Table 8). Mean annual survival rate of fledglings to independence was 73.2% and to one year of age 53.2% (Table 8). Thus, on average

a breeding female added 0.45 yearlings to the population per breeding season. Over a mean observed breeding lifespan of 5.7 years (see above), a female would thus have added an estimated 2.6 yearlings to the population, but many females bred for considerably more than 6 years.

2. Groups

Over the entire study period, mean group size was 6.6 and the mean number of breeding females per group was 2.1 per annum (Table 8). A mean of 2.6 clutches was laid per group in a breeding season. On average, 77.8 % of groups monitored produced at least one fledgling in a season, 68.2% at least one independent juvenile and half at least one yearling. On average, 1.7 fledglings were produced per group in a season, which at the survival rate alluded to above would have resulted in an addition to the population of an estimated 0.9 yearlings per year.

Group size, the number of breeding females and the production of fledglings and yearlings all varied among years in most groups (Table 9 provides a detailed summary). The proportion of breeding seasons in which at least one fledgling

Table 8

Annual variation in productivity parameters in Guildford magpie population, 1996-2005. Data are variously means ($\pm$ standard error), ranges, percentages and sample sizes (in parentheses). Young were considered independent at ~ 2 months old.

Year	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	All Years
Number of groups	12	14	12	13	13	14	14	14	15	14	135 group-years
Mean group size	6.1 $\pm$ 0.56 4-10	6.4 $\pm$ 0.75 3-11	6.5 $\pm$ 0.88 3-12	6.9 $\pm$ 0.87 3-13	5.9 $\pm$ 0.84 2-12	6.3 $\pm$ 0.71 3-10	6.4 $\pm$ 0.74 2-11	6.5 $\pm$ 0.73 2-11	5.9 $\pm$ 0.73 2-10	6.6 $\pm$ 0.89 2-13	6.6 $\pm$ 0.24 2-13
Mean number of breeding females per group	1.58 $\pm$ 0.23 0-3	1.57 $\pm$ 0.20 0-3	2.17 $\pm$ 0.32 1-4	2.00 $\pm$ 0.32 1-5	2.23 $\pm$ 0.32 1-5	2.14 $\pm$ 0.29 1-5	2.21 $\pm$ 0.30 1-5	2.07 $\pm$ 0.30 1-5	2.27 $\pm$ 0.30 1-5	2.35 $\pm$ 0.34 1-5	2.07 $\pm$ 0.09 0-5
Mean number of clutches per group	1.82 $\pm$ 0.30	1.64 $\pm$ 0.23	2.42 $\pm$ 0.31	2.38 $\pm$ 0.35	2.38 $\pm$ 0.31	2.71 $\pm$ 0.40	2.93 $\pm$ 0.52	2.86 $\pm$ 0.48	2.67 $\pm$ 0.44	3.50 $\pm$ 0.65	2.55 $\pm$ 0.14
Percent breeding attempts produced ≥ 1 fledgling(s)	56.5	87	66.7	29	54.8	47.4	56.1	30	48.7	36.7	48.8
Percent groups produced ≥ 1 fledgling(s)	66.7	85.7	83.3	61.5	92.3	78.6	100	64.3	60	85.7	77.8
Percent groups produced ≥ 1 independent young	66.7	71.4	75	46.2	92.3	64.3	71.4	64.3	60	71.4	68.2
Percent groups produced ≥ 1 yearling(s)	50	21.4	66.7	23.1	76.9	64.3	50	57.1	46.7	50	50.4
Mean number of fledglings produced per breeding attempt	0.70 $\pm$ 0.15 0-2 (24)	1.09 $\pm$ 0.14 0-3 (23)	1.07 $\pm$ 0.18 0-3 (27)	0.42 $\pm$ 0.13 0-2 (33)	1.06 $\pm$ 0.21 0-4 (31)	0.63 $\pm$ 0.13 0-2 (38)	0.76 $\pm$ 0.14 0-4 (41)	0.35 $\pm$ 0.09 0-2 (40)	0.64 $\pm$ 0.12 0-2 (39)	0.53 $\pm$ 0.12 0-2 (49)	0.69 $\pm$ 0.05 0-4 (345)
Mean number of fledglings produced per female	0.84 $\pm$ 0.16 0-2 (19)	1.14 $\pm$ 0.19 0-4 (22)	1.11 $\pm$ 0.18 0-3 (27)	0.50 $\pm$ 0.15 0-2 (26)	1.14 $\pm$ 0.22 0-4 (29)	0.80 $\pm$ 0.19 0-5 (30)	1.00 $\pm$ 0.17 0-4 (31)	0.48 $\pm$ 0.12 0-2 (29)	0.71 $\pm$ 0.14 0-2 (34)	0.74 $\pm$ 0.15 0-2 (34)	0.84 $\pm$ 0.05 0-4 (281)
Mean number of fledglings produced per group	1.33 $\pm$ 0.38 0-4	1.79 $\pm$ 0.37 0-5	2.42 $\pm$ 0.58 0-6	1.00 $\pm$ 0.32 0-4	2.54 $\pm$ 0.55 0-6	1.71 $\pm$ 0.46 0-5	2.21 $\pm$ 0.46 0-7	1.00 $\pm$ 0.26 0-3	1.60 $\pm$ 0.43 0-4	1.86 $\pm$ 0.36 0-4	1.74 $\pm$ 0.14 0-7 (135)
Mean number of independent young produced per group	1.17 $\pm$ 0.35 0-4	1.36 $\pm$ 0.33 0-4	1.75 $\pm$ 0.43 0-4	0.62 $\pm$ 0.21 0-2	2.15 $\pm$ 0.49 0-6	1.00 $\pm$ 0.38 0-5	1.36 $\pm$ 0.31 0-3	0.79 $\pm$ 0.21 0-2	1.27 $\pm$ 0.40 0-4	1.36 $\pm$ 0.31 0-4	1.27 $\pm$ 0.11 0-5 (135)
Mean number of yearlings produced per group	1.00 $\pm$ 0.37 0-4	0.64 $\pm$ 0.31 0-4	1.33 $\pm$ 0.36 0-3	0.31 $\pm$ 0.18 0-2	1.62 $\pm$ 0.42 0-5	0.93 $\pm$ 0.32 0-4	0.93 $\pm$ 0.30 0-3	0.57 $\pm$ 0.17 0-2	0.93 $\pm$ 0.35 0-4	1.07 $\pm$ 0.34 0-4	0.93 $\pm$ 0.10 0-5 (135)
Percent fledglings became independent	87.5	76	72.4	61.5	84.9	58.3	61.3	78.6	79.2	73.1	73.2
Percent independent young became yearlings	85.7	47.4	76.2	50	75	92.9	68.4	72.7	73.7	79	72.7
Percent fledglings became yearlings	75	36	55.2	30.8	63.6	54.2	41.9	57.1	58.33	57.7	53.2

was produced ranged from 20 to 100% among groups monitored for ≥ 8 years and the proportion in which at least one yearling was produced from 10 to 90%. The mean number of fledglings produced per season varied among groups from 0.4 to 4.6 (Table 9). This metric was positively correlated with the mean number of breeding females in the group ($r_{(11)} = 0.796$, $P < .01$), but interestingly not with mean group size ($r_{(11)} = 0.511$, $P > .05$). The mean number of yearlings produced per season also varied among groups from 0 to 1.4; it was positively correlated with the average number of breeding females in the group ($r_{(11)} = 0.566$, $P < .05$) and with mean group size ($r_{(11)} = 0.725$, $P < .01$). The total number of yearlings produced by a group over the whole study period varied widely from just 1 to 14 in 10 years. For the 11 groups monitored over 10 successive years, there were positive correlations between the total number of yearlings produced per group and (a) the average number of breeding females in the group ($r_{(9)} = 0.635$, $P < .05$) and (b) mean group size ($r_{(9)} = 0.767$, $P < .01$).

DISCUSSION

Age at first breeding and breeding lifespan of females

Most females in our study whose age at first breeding was accurately determined first bred when 2-3 years old. There are few other reliable estimates of this metric for magpies, as most studies have been relatively short and in some populations young disperse from the natal territory at < 1 year of age (Kaplan 2020) and are difficult to trace. However, Veltman and Carrick (1990) noted that 18 females in their Canberra, Australian Capital Territory (ACT) study first bred at 2-7 years old and 61% had bred by 3 years of age, possibly indicating an even greater average delay in the age of first breeding than that apparent in the present study.

Guildford females attempted to breed in from 1 to all 12 seasons (mean 6) of our investigation and some probably bred for > 12 seasons during their entire lifespan. In Carrick's (1972)

Table 9

Inter-group variation in productivity parameters in the Guildford magpie population, 1996-2005. Data are means ($\pm$ standard error) and ranges. Total numbers of yearlings produced during study in bold font. F = fledgling, Y = yearling.

Group	No. years monitored	Group size mean range	No. breeding females mean (SE) range	No. fledglings produced mean (SE) range	No. yearlings produced mean (SE) range	Percent years in which produced at least one young	
						F	Y
FM	10	9 6-13	3.2 (0.39) 1-5	1.9 (0.35) 1-4	1.3 (0.3) 0-3 13	100	80
FP	10	3.2 2-4	1.1 (0.2) 1-2	0.70 (0.21) 0-2	0.1 (0.1) 0.1 1	50	10
HC	10	6 4-8	2.2 (0.2) 1-3	2.7 (0.65) 0-6	1.30 (0.52) 0-5 11	90	50
HR	10	10.8 9-13	2.10 (0.18) 1-3	1.60 (0.4) 0-4	1.4 (0.43) 0-4 14	80	70
LP	10	4.5 4-5	1.6 (0.16) 1-2	0.4 (0.22) 0-2	0 0	20	0
MM	10	9.1 6-11	3.9 (0.41) 2-5	4.6 (0.43) 2-7	1.4 (0.37) 0-4 14	100	80
NH	10	7.5 6-9	2.4 (0.27) 1-3	1.8 (0.44) 0-4	0.90 (0.41) 0-4 9	90	50
PG1	10	7.9 4-12	2.5 (0.31) 1-4	2.2 (0.42) 1-4	1.8 (0.39) 0-4 18	100	90
SM	10	5.2 3-7	2.00 (0.21) 1-3	1.8 (0.42) 0-4	1.0 (0.33) 0-3 10	80	60
WB	10	4.9 2-7	1	1.4 (0.16) 1-2	0.9 (0.23) 0-2 9	100	70
OV	10	7.3 6-10	1.2 (0.25) 0-2	1.00 (0.42) 0-4	0.8 (0.42) 0-4 8	50	40
GG	9	5.56 2-12	2.11 (0.39) 1-4	2.56 (0.5) 0-5	1.44 (0.53) 0-4 13	88.9	55.6
PG2	8	3.63 3-6	1.88 (0.13) 1-2	0.75 (0.25) 0-2	0 0	62.5	0
VM	5	3	1.8 (0.2) 1-2	0.4 (0.2) 0-1	0 0	40	0
WS	2	3	1	1 (1) 0-2	1 (1) 0-2 2	50	50

twelve-year Canberra study, the record number of breeding seasons recorded for a female was eleven. He also roughly estimated magpies' lifespan in Canberra to be ~20 years, whilst Kaplan (2020) reported that a breeding pair in New South Wales was bonded for 17 years and Pike *et al.* (2019) noted that some breeding birds at Guildford (that we banded) were at least 23 years old at the time when they studied them. Thus, it may be common for female magpies to breed for ~10 seasons and some possibly for as many as 20+ seasons, but this requires further investigation.

Magpies at Guildford mostly did not breed in their first potential breeding season (i.e. in the year after they fledged),

went through a series of sub-adult plumages in their early life (Rowley *et al.* in prep. b) and then often had a protracted breeding life. We speculate that this syndrome is best explained by the Delayed Investment Hypothesis (Hawkins *et al.* 2012), which views delayed acquisition of adult plumage as part of an adaptive life history strategy in long-lived species that is associated with delayed reproductive investment and is driven by competition. It is thought that sexual competition is particularly intense in co-operative breeding systems (but see Beauchamp 2003) and therefore it may benefit young birds in long-lived, co-operatively breeding species to delay breeding until they are competitive. It is unlikely that sub-adult plumage aids mimicry or crypsis (Hawkins *et al.* 2012) very significantly in magpies

Table 10

Initiation of breeding by Australian Magpies at five latitudes in Australasia extracted from literature. NZ= New Zealand.

Source	Location and latitude (°S)	Timing of breeding
Rollinson and Jones (2003)	Brisbane, Qld 27.4705	Mean nest building initiation date: 19 Jul – 10 Aug Mean clutch initiation date: 5 Aug – 23 Aug
Present study	Guildford, WA 31.8994	Clutch initiation: all clutches 12/21 Aug – 1/10 Dec 1st clutches 12/21 Aug – 1/10 Nov
Carrick (1972)	Canberra, ACT 35.2809	Clutch initiation: 1st clutches 22 Aug-15 Sep Breeding season: Aug-Nov
Durrant and Hughes (2005)	Rowsley, Vic 37.7216	Breeding season: Jun-Nov Fledging: mid-Sep to late Nov (so extrapolated laying dates ~ 14 Jul-28 Sep)
Veltman (1984)	Linton, NZ 40.4322	Nest building: early Jun Oviposition: from early Aug

and more probable that it is an honest signal of subordinate status employed adaptively in competition with adults and sub-adults of older age-classes over access to mates or food (Dale 2006).

Breeding phenology

Birds are predicted to meet the high energy demands of breeding by timing reproduction so that it coincides with the peak abundance of their major food items (Burr *et al.* 2016). The degree of seasonality in several environmental parameters that influence birds' food abundance and foraging activity, such as ambient temperature and photoperiod, increases with latitude and is often accompanied by disparities in the timing of seasonal events such as breeding. Numerous studies have demonstrated a later initiation of breeding inter- and intra-specifically in land birds and sea birds at higher latitudes in the northern hemisphere (e.g. Baker 1938; Sanz 1998; Wanless *et al.* 2008; Carillo and Gonzalez-Davila 2009; Burr *et al.* 2016).

The composite geographical range of the magpie in Australasia extends over ~26° of latitude from the tropics to well into the temperate zone (Menkhorst *et al.* 2017). It might therefore be conjectured that, given the substantial latitudinal gradient in the timing of breeding of many northern hemisphere bird species outlined above, magpies would start breeding somewhat later in the more southerly parts of the species' range. Initiation of clutches in the present study at Guildford (31.8994°S) occurred from late winter to early summer, with a late winter-early spring peak. Females' first clutches of the season (~68% of all those laid) were initiated from late winter to late spring, again with a late winter-early spring peak. This timing broadly concurs with that reported for magpies in four other Australasian locations spread over 13° degrees of latitude from the subtropics to 40°S (Table 10) and with the general summaries for Australasia provided by Higgins *et al.* (2006) and Kaplan (2020).

There is a significant trend for magpie breeding to be initiated a few days later at higher latitudes in Australia (Gibbs *et al.* 2011). However, Gibbs (2007) concluded that the timing of the species' breeding is broadly very similar continent-wide (despite huge latitudinal differences across the species' range in climate and seasonality) and our results further support this conclusion. The lack of a more pronounced latitudinal gradient is interesting, particularly as it appears to be part of a possibly broader trend among Australian land birds (Gibbs *et al.* 2011).

However, two caveats must be borne in mind with respect to this issue: 1) that the main Australasian landmass and the southerly extent of the magpie's range extend only to ~46°S, a much lower latitude than that of many of the locations for which northern hemisphere avian breeding phenology records have been obtained, and 2) that the precision of many of the published records of magpie breeding may be insufficient to permit detection of a modest latitudinal gradient. More data on magpie breeding phenology in tropical Australia and Papua-New Guinea would be helpful in further exploring this issue.

Nest sites and nests

In the present study, most nests were 10-20m above ground level in tall eucalypts, similar sites to those recorded for Canberra by Carrick (1972) and the Brisbane area by Rollinson and Jones (2003); these authors also noted that some nests were built in artificial structures, something we never observed in our study. Kaplan (2020) noted that nests in mature eucalypts in Victoria and New South Wales were also about 10-15m above ground level, but those in deciduous trees and pines were only 4-6 m above the ground. Nesting well above ground level precludes nest predation by ground predators, but not of course by scansorial (e.g. Varanid lizards), arboreal and avian (e.g. Australian Ravens *Corvus coronoides*) predators of magpie young (Kaplan 2020). Eucalypts may commonly be used for nesting because they are often the most numerous tall trees in the open habitats inhabited by magpies in Australia.

Magpie nests at Guildford comprised a deep cup with a soft lining set on a twig platform and often contained anthropogenic materials in the outer layer, as documented elsewhere in Australia (Kaplan 2020). Although nests were usually well spaced, in plural-breeding territories two or three females sometimes nested close together simultaneously in the same tree or tree cluster, a phenomenon also recorded elsewhere in Western Australia (Fulton 2006) and in New South Wales (Kaplan 2020).

Care of offspring

1. Incubation and nestling stages

In the more than 300 breeding attempts observed, we noted that only females built the nest, incubated eggs and brooded nestlings, an apparently universal pattern in magpies

(Robinson 1956; Carrick, 1972; Veltman, 1984; Hughes *et al.* 1996; Higgins *et al.* 2006). However, a male sometimes fed an incubating female and 'guarded' the nest area, as noted by Carrick (1972) in Canberra, Hughes *et al.* (1996) at Seymour, Victoria and Kaplan (2020) more generally.

The 21-day median incubation period at Guildford agreed quite closely with estimates for Coolup, Western Australia, Canberra and the Brisbane region (Robinson 1956; Carrick 1972; Rollinson and Jones 2003). The observed nestling period duration (c. 30 days) concurred reasonably closely with a later estimate for this population (Pike *et al.* 2019) and one for Canberra (Carrick 1972), but was a few days shorter than estimates for Coolup (34 days, Robinson 1956) and the Brisbane region (34.5 – 38.2 days, Rollinson and Jones 2003). Some intra-specific variability in avian nestling period duration is not unexpected (e.g. Soler 1988), but overall it appears that the mean durations of the incubation and nestling periods are quite similar throughout the magpie's range.

2. Provisioning of nestlings

Most feeding of nestlings at Guildford was by the presumed mother, but adult males and other adult females sometimes contributed, as noted in some other group-living magpie populations elsewhere in Australasia (Carrick 1972; Veltman 1984; Hughes *et al.* 1996; Finn and Hughes 2001; Rollinson and Jones 2003; Durrant 2004).

Some females in our study received no adult male help in feeding their nestlings in a specific season, but those that did were helped by up to at least two males. Females being assisted in feeding their nestlings by more than one male during a season has also been recorded at Seymour, Victoria in co-operatively breeding white-backed magpies (Hughes *et al.* 1996; Finn and Hughes 2001). In the present study, those females that were assisted by just one specific adult male usually fed the nestlings much more than did the male. Pike *et al.* (2019) also found that typically a Guildford mother invested more in her nestlings than did the social father, whose certainty of paternity was low because of the high level of extra-group paternity in this population (Hughes *et al.* 2003), and Durrant (2004) reported a similar trend among white-backed magpies at Rowsley, Victoria. At Guildford, an adult female occasionally fed nestlings other than her own, particularly after her own breeding attempt had failed. The resultant phenomenon of up to two adult females feeding nestlings of one brood has also been recorded at Seymour (Hughes *et al.* 1996; Finn and Hughes 2001). Some adult males appeared to play no role in feeding nestlings in a specific season; those that helped to provision nestlings usually did so at either one nest or two in parallel or sequentially.

3. Provisioning of fledglings

A few females provisioned their fledglings very little in a specific season. Nonetheless, overall most feeding of fledglings was performed by their presumed mother, although some involvement of one or two adult males, other adult females and immature group-members was observed, as in later studies of this population (Durrant 2004; Pike *et al.* 2019) and investigations of white-backed magpies in Victoria (Hughes *et al.* 1996; Finn and Hughes 2001; Durrant 2004). Some adult males in our investigation fed the fledglings of at least two females in the same breeding season.

Pike *et al.* (2019) showed in a two-year study of the Guildford population that the tendency to care for young by individuals other than their putative parents was influenced by (a) group size (more helping in smaller groups), (b) chick age (helping more common at the fledgling than the nesting stage) and (c) the helper's sex, age (females helped more than males and juveniles) and foraging efficiency (more efficient foragers fed more biomass to young).

Many aspects of the co-operative nestling and fledgling provisioning regimes at Guildford are clearly not unique, similar patterns having been recorded in Victoria and the ACT particularly.

4. Possible ecological factors favouring co-operative breeding

Our findings on helping behaviour augment current knowledge of how its nature and occurrence vary among magpie populations across Australasia. Intriguingly, there appear to be two essentially contrasting environments that favour cooperative breeding in birds: (1) relatively stable, productive, 'saturated' environments in which early dispersal and attempted independent breeding or 'floating' are both poor fitness options (the ecological constraints or habitat saturation model), and (2) highly variable, unpredictable environments in which successful breeding is difficult without helpers because of resource limitation (the 'hard life' hypothesis) (Koenig 2017). Shen *et al.* (2017) suggest that this dichotomy may be explicable through the Dual Benefits Hypothesis. They propose that members of populations experiencing habitat saturation in spatially heterogeneous environments may benefit from group-living mainly through group defence of resources, whereas members of groups that form because grouping helps to overcome breeding difficulties imposed by resource limitation in temporally variable environments may benefit mainly from cooperative behaviours. Given the geographic variation in group size and composition, dispersal, extra-group paternity and particularly the tendency to breed cooperatively, the Australian Magpie offers an exciting opportunity to elucidate the ecological factors driving the evolution of cooperative breeding which has yet to be fully realised, despite the large volume of published research on the species (Kaplan 2020).

5. Long-term patterns of provisioning assistance

Long-term patterns of assistance given to female magpies in feeding their offspring have not been extensively documented because most investigations have typically lasted only 2-3 years; our observations therefore provide rare, long-term data that address this knowledge gap. Some females whose breeding we observed over several years received little or no adult male assistance in provisioning nestlings or fledglings over the entire monitoring period, whereas others were assisted by up to six different males during the proportion of their breeding lifespan that we monitored (up to 10 years). Some adult males did not feed nestlings or fledglings very often, but some of those that did fed the broods of multiple females (up to 5) during the portion of their breeding lifespan that was covered by our study. Some males fed the broods of a specific female in many breeding attempts (up to 7) over several years, suggesting perhaps that some long-term pair bonds occur within this group-living, plural-breeding society, although these males also fed the young of other females to a lesser extent.

Table 11

Breeding success and productivity metrics for magpie populations in Australasia extracted from literature. NZ = New Zealand, NRS = Nest record scheme, a.l. = at least and No. = number.

Variable	Metric	Source; location	Data
Fledging success	a.l. 1 nestling in brood fledged	Rollinson & Jones (2003) Brisbane Region	58-73% of broods
		Pike <i>et al.</i> (2019) Guildford	47% of broods
	Percent of nestlings fledged	Veltman (1984) NZNRS	53% of nestlings (n=7 broods)
	Percent eggs produced fledglings	Veltman (1984) Linton, NZ	38% of eggs
Survival rate to end of breeding season or independence	a.l. 1 young in brood survived	Rollinson & Jones (2003) Brisbane region	40-73% of broods
		Pike <i>et al.</i> (2019) Guildford	22% of broods
	No. young survived	Carrick (1972) Canberra	0.5 young per adult female
Survival rate to adulthood	Percent hatched young reaching adulthood	Carrick (1972) Canberra	14.3% of young (in permanent groups)
Production of fledglings	No. fledglings produced per group/year	Hughes <i>et al.</i> (1996) Moggil, Qld	1.43-1.67
		Seymour, Vic.	1.89-2.89
		Rollinson and Jones (2003) Brisbane region	1.0-1.6
		Veltman (1989) Linton, NZ.	1.2
		Durrant (2004) Rowsley, Vic	1.5-1.8 (productive groups only)
Production of independent young	No. independent young produced per adult female/year	Carrick (1972) Canberra	0.56 (in permanent groups)
		Veltman (1984) Linton, NZ	0.9-1.6
		Rollinson and Jones (2003) Brisbane region	0.7-1.0

Productivity

1. Breeding attempts per female per season

Most adult females made only one breeding attempt per season, just 21.5% of clutches being second or third attempts of the season and only 6% of attempts occurring after earlier success. Rollinson and Jones (2003) found that only 16-20% of suburban (and no rural) females in the Brisbane region laid a second clutch, apparently always after earlier failure. Carrick (1972) noted that some Canberra females re-nested after failure, but successful rearing of two broods in a season was not observed. The negligible tendency among magpies generally to re-nest after earlier success is not surprising, given that offspring care can extend for at least three months post-fledging (Kaplan 2020). Successfully rearing a second brood after earlier success would therefore usually require a breeding female to forego

provisioning her first brood of fledglings; this phenomenon was seen in our study, but only occasionally.

2. Brood fledging success

Fledging success (at least one nestling in a brood fledged) in our study was nearly 50% overall, but there was much annual variation. Interestingly, using the same success criterion, Pike *et al.* (2019) recorded a very similar percentage success to our value in a later two-year investigation at Guildford (Table 10). However, Rollinson and Jones (2003) documented rather higher values (58-73%) in suburban and rural populations studied over two seasons in the Brisbane region (Table 10). Veltman (1984) reported that the percentage of nestlings that fledged (as opposed to at least one brood member fledging) was estimated as 53% from the New Zealand Nest Record Scheme, but the sample size was small (Table 10). Most nesting failure in our investigation

occurred at the incubation and early nestling stages (Table 7), but the reasons for failure were mostly unclear. Carrick (1972) also reported high failure rates in the incubation and early nestling stages in Canberra and attributed them speculatively to avian predation and adverse weather conditions.

3. Brood survival to independence and beyond

At least one fledgling survived to independence (in January) in 73% of broods in the present study; however, Pike *et al.* (2019) recorded a much lower rate (22%) in a later, smaller study of 11 breeding groups over two seasons in the same study site, although the reason for the disparity is unclear. Rollinson and Jones (2003) reported rates ranging from 40–73% of broods having some offspring survival to independence in the Brisbane region in two seasons (Table 11). Carrick (1972) noted that only 14% of nestlings survived to adulthood in Canberra, but we found that at least one fledgling survived to one year of age in just over half of the broods at Guildford.

4. Female and group productivity

Individual females in our investigation produced an estimated mean of 0.8 fledglings, 0.6 independent young and 0.5 yearlings per season. Estimates of the annual production of independent young by females in other magpie populations range from 0.6 to 1.6 (Table 11). We calculated that an adult Guildford female breeding for the mean reproductive lifespan observed in our study (~6 seasons) would have added 2.6 yearlings to the population, and some females bred for considerably longer than six years. Carrick (1972) estimated for the Canberra population that a female in her breeding lifespan might produce 8.4 offspring that survived to breeding age, but his estimate is based on a possibly unrealistic estimate of hatching success.

In our study, mean group size early in the breeding season was ~7, the mean number of breeding females per group was ~2 and ~2.5 clutches were laid per group in a season. On average, 1.7 fledglings were produced per group in a season. This fledgling production level is lower than that of similarly-sized groups (7–8 members) at Seymour, comparable to that of much smaller groups (2–2.5) at Moggill and Brisbane, Queensland, but higher than that of smaller groups (3.7) at Linton, New Zealand (Veltman 1989; Hughes *et al.* 1996; Rollinson and Jones 2003) (Table 10). This variability is not surprising given that there would probably be underlying temporal and habitat variation. We calculated that, on average, a Guildford group produced 0.9 yearlings per year, but there are few data for other populations available for comparison.

There is considerable variability in productivity parameters among Australasian magpie populations and there are not currently sufficient comparative data to determine confidently whether the Western Magpies at Guildford exhibited a distinct productivity profile.

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