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ABSTRACT

Context. Sex and age are frequently proposed as drivers of a number of behavioural and demographic patterns that can have important consequences for population dynamics including access to mates, sexual selection, parental care and lifetime productivity. Sex and age might also be important in shaping the movement patterns and colonisation processes of social species moving into vacant habitat. Such information is critical for the management of strongly interacting species such as the noisy miner (*Manorina melanocephala*), which structure ecological communities through aggressive exclusion of other taxa from areas that they occupy. **Aims.** In *Manorina* colonies, young females are usually dispersive, while males remain in the natal colony as the philopatric sex. Following removal of individuals from an area, we aimed to determine whether female-biased dispersal, particularly of young females, would result in a more equal sex ratio and a younger age structure in the recolonising population. **Methods.** These predictions were tested by anatomically ageing and sexing 1856 noisy miners that had been experimentally culled in two regions of New South Wales, Australia, to reduce the aggressive impact of this species on other native species. **Key results.** Prior to removal, noisy miner populations were significantly male-biased in both regions (57% and 60%); however sex ratios after each of two removal episodes no longer differed from parity. Immature birds were a dominant feature (65%) of recolonising populations in both regions, however, the age structure of recolonising populations was different in each region, mostly likely due to the respective timing of culls during the year. Furthermore, the culling response in terms of age-specific sex ratio varied between regions. After the final cull, the sex ratio of mature birds had fallen to parity in one region but had become even more male biased (68%) in the other region. There was no sex-ratio bias among immature birds before or after culling. **Conclusion.** These results confirm the expectation that immature birds are more likely to be colonisers, but the expectation of greater female dispersal was equivocal. **Implications.** The differences in response between regions may reflect variation in population density, landscape connectivity or seasonality, highlighting challenges when implementing culling programs for conservation management.

Keywords: age structure, dispersal, lethal management, *Manorina melanocephala*, noisy miner, recolonisation, sex ratio, superabundant species.

Introduction

Sex ratio variation is a fundamental component of wild population dynamics (Eberhart-Phillips *et al.* 2018) and has extensive implications for the ecology, behaviour and life history of populations (Székely *et al.* 2014). Adult sex ratios can determine the social structure of the population where mating system traits such as divorce, extra-pair copulations and paternal care can be altered due to a biased sex ratio in the population (Liker *et al.* 2014; Remeš *et al.* 2015; Eberhart-Phillips *et al.* 2018). Consequently, sex ratio is important for population productivity (Liker *et al.* 2014) and may result in decreased fitness of a particular sex (Grayson *et al.* 2014). Sex ratio and sex allocation

are therefore important metrics for management and conservation practices (Komdeur 1994; Baumgardt *et al.* 2013; Reichard *et al.* 2014; Székely *et al.* 2014).

The overall sex ratio of a population is influenced by age structure, being dependant on the proportion of each age group in the population and the variation between adult and non-adult sex ratios (Székely *et al.* 2014). These population attributes may influence movement patterns and recolonisation of new territories (Kokko *et al.* 2006) through sex-specific and age-specific philopatry. For example, in most bird species males tend to stay in their natal home range, whereas first-year females seek new territories (Kokko *et al.* 2006). Therefore, different sexes provide different fitness payoffs for parents, and sex-related dispersal could be a major factor that determines how parents invest in each sex (Hatchwell 2009).

Sex-related parental investment can happen by facultatively adjusting sex ratio in favour of production of the beneficial sex (Ewen *et al.* 2003), or during the rearing stage through differential resource allocation (Ridley and Huyvaert 2007). This is particularly important in cooperatively breeding species, in which offspring receive care from other individuals within a group in addition to parents. In these species, sex-biased investment can be determined by group size, as parents and helpers that might benefit from a larger group size would increase their fitness by preferentially investing in the philopatric sex (Ewen *et al.* 2003; Ridley and Huyvaert 2007; but see McDonald *et al.* 2010). Although producing more young of the helping sex might generally be favoured, producing more of the dispersive sex may be favoured when territories are at capacity.

Dispersal strategies might also be influenced by the age structure of the populations. If young birds have to queue to get a breeding position, then they may disperse to new territories with a smaller queue, allowing them to become part of the breeding population sooner (Wiley and Rabenold 1984; Nelson-Flower *et al.* 2018). Through their role in dispersal, natality and mortality, population age and sex composition have considerable influence on future reproduction (Alexander 1958) and so it is particularly important to understand these population attributes when undertaking management intervention on strongly interacting species, i.e. species that have disproportionately large ecological effects given their abundances (Thomson *et al.* 2015).

The noisy miner (*Manorina melanocephala*), a strongly interacting Australian honeyeater, has been recognised in *Key Threatening Process* listings on account of its adverse impact on threatened bird species (NSWSC 2013; TSSC 2013). Noisy miners have been described as a 'despotic species' (Mac Nally *et al.* 2012) because they aggressively exclude almost all smaller birds from their territories (Maron *et al.* 2013). They are cooperative breeders and live in aggregations of up to several hundred birds organised into tribes or coteries of 10–25 individuals within a colony (Higgins *et al.* 2001). Colony members cooperate in various

contexts, including the feeding of young (Higgins *et al.* 2001; Barati *et al.* 2018a), mobbing of predators (Arnold 2000) and defence of the colony's territory from intra and interspecific intruders (Dow 1977). In natural, well established colonies there is a male-biased sex ratio (Barati *et al.* 2018a). It is thought that this is due to females dispersing from established colonies, with males being the philopatric sex, as occurs in the congeneric Bell Miner (*Manorina melanophrys*) (Dare *et al.* 2007, 2008).

Culling of noisy miners has been trialled as a management strategy to recover depleted populations of small woodland birds, but outcomes have been inconsistent and further research is required to understand the circumstances under which rapid recolonisation of noisy miner-vacated habitat does, and does not, occur (Melton *et al.* 2021). The key to this understanding is rooted in the drivers of dispersal, of which age and sex composition are fundamental considerations.

The aim of this study was to examine individuals removed in a large scale cull of noisy miners to determine how age structure and sex ratios varied between the initial population and subsequent recolonised populations. Specifically, we tested the following predictions based on the known social structure of noisy miner colonies: (1) *Recolonised populations will have a significantly higher proportion of females than were present in the original population*. This prediction is based on males being more philopatric in noisy miner social systems and thus less likely to seek out vacant habitat than females. (2) *Recolonised populations will have a significantly higher percentage of immature birds than were present in the original population*. This prediction is based on the queuing hypotheses whereby younger birds will have faster access to breeding opportunities through accessing new habitat than by waiting within an established colony.

Materials and methods

Study sites and sample collection

The study was conducted in two distinct regions of New South Wales, Australia (Fig. 1*a*), selected to capture variation in landscape cover of remnant eucalypt woodland, which is the primary habitat of noisy miners and may explain some of the variation in noisy miner behaviour (Melton *et al.* 2021). The Bundarra study region (Fig. 1*b*) is situated in the New England Tablelands Bioregion (Thackway and Cresswell 1995) and has 31% cover of eucalypt forest and woodland, compared with 13% cover in the Fifield study region (Fig. 1*c*), which is situated in the South Western Slopes Bioregion. The two regions also differ in annual rainfall which is higher at Bundarra than Fifield (Fig. 2). Rainfall in the year preceding sample collection was typical of long-term means.
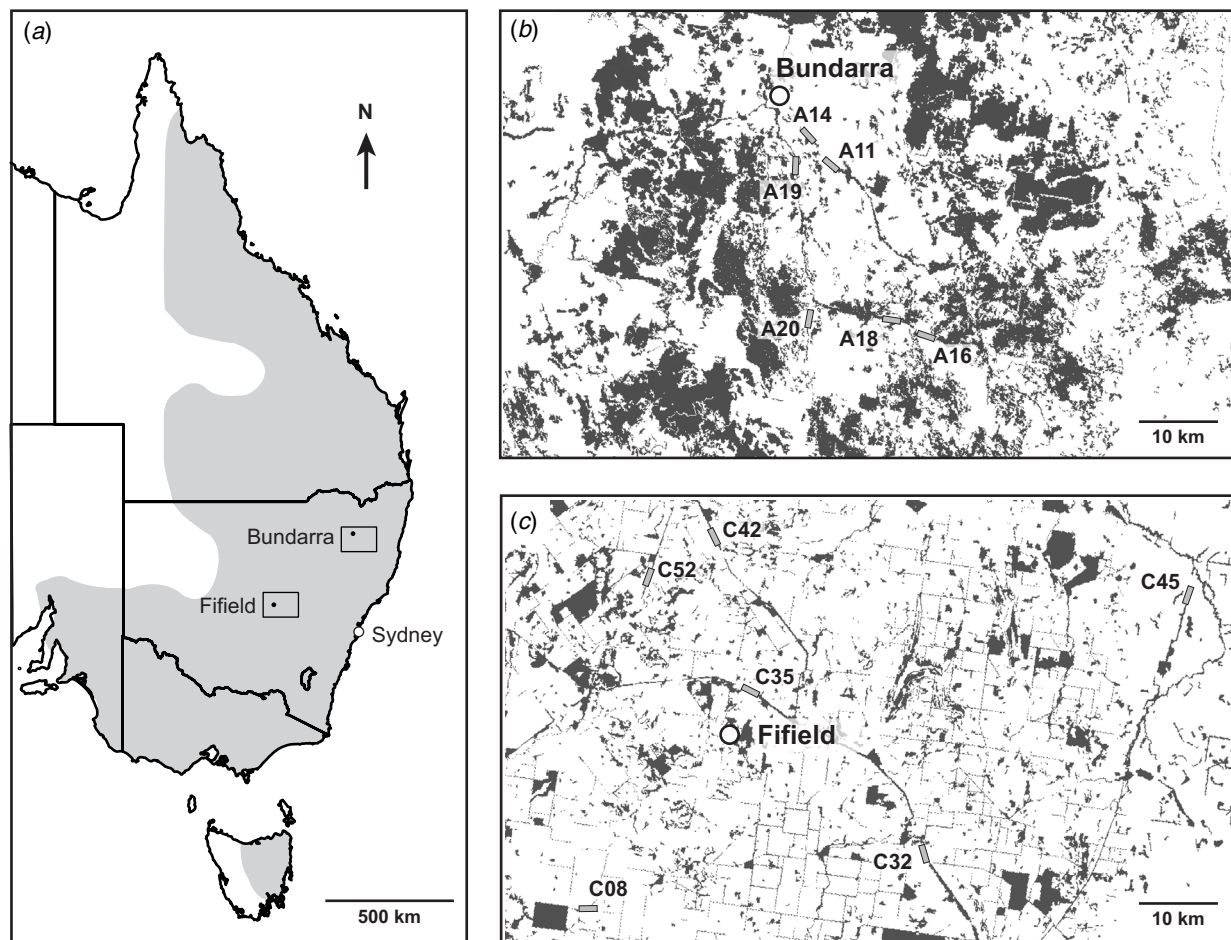
142

Fig. 1. (*a*) Location of the two study regions in eastern Australia near the towns of (*b*) Bundarra and (*c*) Fifield, New South Wales. The extent of eucalypt forest and woodland (*b* and *c*) is indicated by dark shading (data from Department of the Environment 2012) and the approximate distribution of the noisy miner in eastern Australia (*a*) is delineated with light shading (data from BirdLife International 2018).

Samples used in this study were collected as a consequence of a noisy miner removal experiment investigating the restoration of woodland bird communities (see Davitt *et al.* 2018 for details). In brief, a 12-gauge shotgun was used to systematically remove noisy miners from six separate linear strips of remnant eucalypt woodland in each region. All removal sites were at least 50 m in width, 2 km in length, and ranged between 16 and 50 hectares in area. Three removal episodes were implemented at each site (Fig. 2), with the first, second and third removals at Fifield occurring from 19–24 August 2015; 12–17 September 2015; and 12–19 April 2016 respectively. The Bundarra removal episodes occurred after the corresponding Fifield removals, from 14–20 November 2015; 4–10 December 2015; and 3–10 May 2016. These removals yielded three samples of birds from each region termed, hereafter, *Initial, Recolonisation 1* and *Recolonisation 2*.

A trained, licensed shooter accompanied by two experienced ornithologists traversed the length of each site

by foot, using broadcast of noisy miner calls at ~50–100 m intervals to attract noisy miners to trees where they could easily be shot. The three personnel spread out across the width of each site when walking between playback points to detect, shoot and collect all noisy miners encountered. Sites were visited on at least two occasions during each removal period, until the vast majority of noisy miners had been removed from a site (fewer than 10 individuals remaining – Davitt *et al.* 2018). Carcasses were stored frozen until subsequent anatomical analysis to determine age and sex of collected birds.

Noisy miner density was significantly higher ($F_{1,30} = 20.66$, $P < 0.001$) in the Bundarra region than the Fifield region as determined by the number of birds shot per hectare per hour (Fig. 3). We analysed a sample of collected birds (1131 from Bundarra; 725 from Fifield). We attempted to balance sample sizes across all sites and removals, but this was not always possible because of the relatively small number of individuals culled in some sites
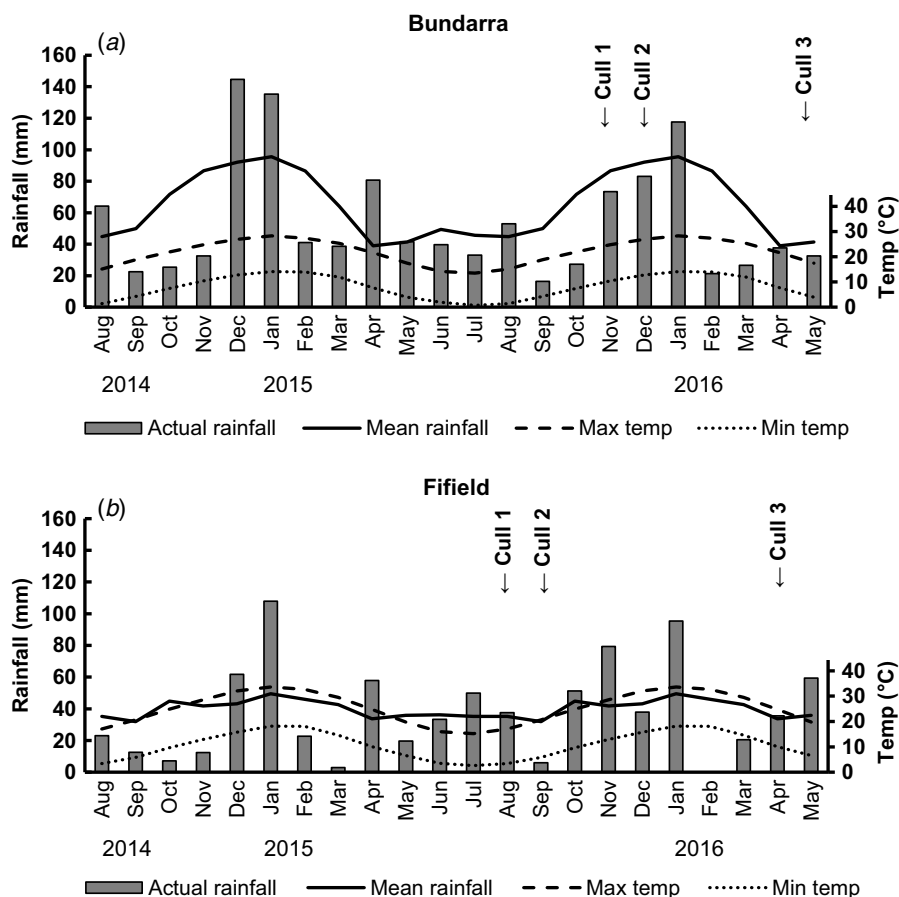
143

Fig. 2. Monthly rainfall (vertical bars) in the year prior to noisy miner removal at (*a*) Bundarra and (*b*) Fifield. Long term monthly averages for rainfall and temperature are superimposed with continuous lines (data from Bureau of Meteorology 2021). The months in which each cull occurred are indicated by arrows.
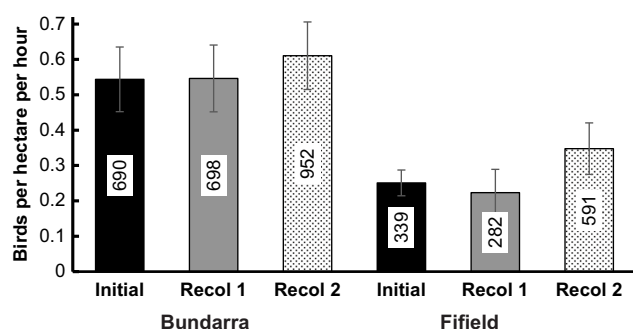

Fig. 3. Variation in mean (±s.e.) culling intensity for three noisy miner removals in two regions. Numbers within the bars indicate the total number of birds culled from six sites in each region. Culling intensity is expressed as the number of birds per hectare per hour to account for differences between individual sites and culls. Differences between regions were significant ($F_{1,30} = 20.66$, $P < 0.001$).

in some periods (e.g. Recolonisation 1 at sites C45 and C52 – Supplementary materials Fig. S1b). Accordingly, sites within each region are pooled in our analysis of the

difference in sex ratio and age structure of the initial and recolonising populations. Within each site × removal combination, birds were selected randomly. (All birds had been wrapped in paper towel and bagged, so they were not visible at the time of selection).

Ageing and sexing birds

Each noisy miner carcass was examined by dissection to determine its sex and age, although a small number of Fifield birds could not be assigned a sex due to extensive shotgun damage to the gonads. Most birds could be sexed by the presence of testes or ovary, but in some cases where gonads were particularly regressed, careful searching for the oviduct was necessary. The sexes of 130 Bundarra birds that were either extensively damaged or had inconclusive gonads were determined using a PCR-based method that focuses on two Chromo-Heli-case-DNA (CHD) binding genes that are found on avian sex chromosomes (Griffiths *et al.* 1998; Kopps *et al.* 2013; Etezadifar 2021).

Age determination was based upon the degree of skull pneumatisation (Pyle *et al.* 1987), assessed by peeling back the cranial skin after making an incision in the crown, and classified as 'minimal', 'partial', or 'complete'. As it is not known at what age the skull of the noisy miner becomes completely pneumatised, an exact age cannot be determined from these characteristics. However, as passerines generally complete pneumatisation by 4–8 months of age (Serventy *et al.* 1967) all individuals with minimal or partial skull pneumatisation were classified as 'immatures' (Dow 1978), and all other individuals were classified as 'mature', recognising that this category may be over-represented as some immatures may consequently be classed as mature.

Analysis of demographic structure

Nominal logistic models (implemented in JMP® v.15 (JMP 2019)) were used to identify differences in sex ratio and age structure between the initial population and recolonising populations 1 month and 6–8 months after the initial removal. Region (Bundarra/Fifield) was also included in the model because there were fundamental differences in the two regions in terms of vegetation cover, climate, and the season in which the various culls occurred.

Where significant main effects and interactions were identified, pairwise nominal logistic models were used to determine which recolonisation events differed from the initial population in terms of age structure and sex ratio. Pairwise models were also used to identify differences in sex ratios from parity.

Ethics statement

This study used specimens collected from a separate study assisted by the New South Wales Government through the Environmental Trust. The initial study was authorised by scientific license S101522 under the NSW National Parks and Wildlife Act, with ethics approval granted by the Australian Museum Animal Care and Ethics under approval number 15/04.

Results

The overall sex ratio of noisy miners sampled in each cull ranged between 41% and 70% with mostly low variability among individual sites located within each region (Fig. S1). However, there was considerable variation between regions in the percentage of immature individuals in each sample, with particularly low numbers of immature birds in the initial population and first recolonisation of sites at Fifield (Fig. S2). The nominal logistic model of age structure identified a significant *Cull × Region* interaction necessitating consideration of separate demographic responses in each region (Table 1). In the Bundarra region 41% of birds in the initial population were immature, which was significantly

Table 1. Results of nominal logistic model to identify variation in age of noisy miners structure (percentage of immatures) associated with cull number (initial/first recolonisation/second recolonisation) and study region (Bundarra/Fifield).

Source	d.f.	Chi-square	P
Cull	2	178.228965	<0.0001*
Region	1	96.5207734	<0.0001*
Cull × Region	2	144.765614	<0.0001*

lower than the percentage of immature birds in both the first and second recolonisation events (Fig. 4a, Table S1). In contrast, only 12% of birds in the initial Fifield population were immature, which was similar to the percentage of immature birds in the first recolonisation event, and significantly lower than the percentage in the second recolonisation event (Fig. 4b, Table S1).

The nominal logistic model of sex ratio (including *Age* in the model) identified a significant effect of *Age*, and also a significant *Age × Cull × Region* effect (Table 2). Accordingly, the variation in sex ratio between recolonisation events must be evaluated separately for each age group in each region (Fig. 5).

The sex ratio of mature birds in the second colonisation event at Bundarra was significantly less male biased than in the initial population (66% male). The sex ratio of the first recolonisation event was also less male biased, but intermediate between the two (Fig. 5a). Mature individuals displayed a significantly male biased sex ratio in the initial population ($\chi^2_1 = 29.90$, $N = 277$, $P < 0.0001$) but the sex ratio did not differ from parity in the first ($\chi^2_1 = 2.97$, $N = 66$, $P = 0.084$) or second recolonisation events ($\chi^2_1 = 0.11$, $N = 152$, $P = 0.740$). For immature birds, there were no significant differences in the sex ratio among recolonisation events (Fig. 5b, Table S1) and none of the immature sex ratios differed from parity.

The sex ratio of recolonising birds at Fifield followed a different pattern from Bundarra. The sex ratio of adult birds (Fig. 5c, Table S1) was significantly lower in the initial and first recolonisation events than in the second recolonisation event. Mature individuals displayed a significantly male-biased sex ratio in the initial population ($\chi^2_1 = 3.95$, $N = 243$, $P = 0.047$) and the second recolonisation event ($\chi^2_1 = 12.0$, $N = 91$, $P < 0.001$), but the sex ratio in the first recolonisation event was not significantly different from parity ($\chi^2_1 = 2.63$, $N = 152$, $P = 0.105$). However, the lack of a significant difference from parity is likely to be a consequence of statistical power, because this sex ratio was equal to that observed in the initial population which did differ significantly from parity and had a larger sample size. As was the case in the Bundarra region, there were no significant differences in the sex ratio of immature birds among recolonisation events (Fig. 5d, Table S1), and none of the immature sex ratios differed from parity.
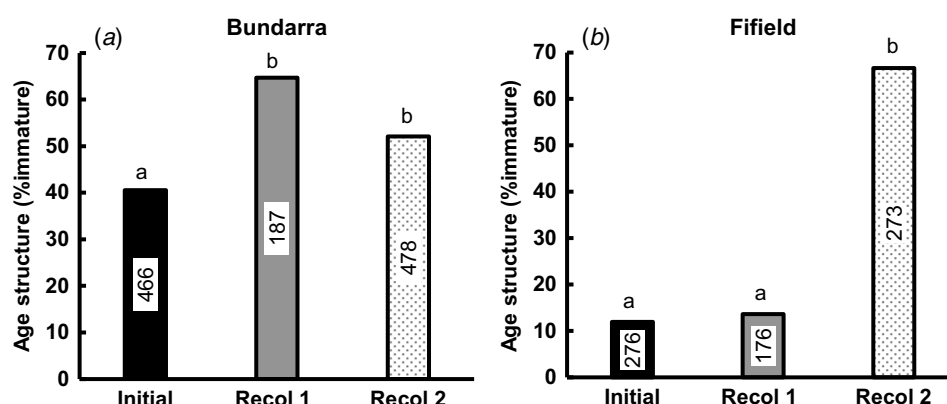
Fig. 4. Variation in age structure between recolonisation events at (*a*) Bundarra and (*b*) Fifield. Bars sharing the same letter within histograms are not significantly different (*P* < 0.05). Numbers within the bars indicate sample size. Refer to text for timing of each sample, which varied between regions.

Table 2. Results of nominal logistic model to identify variation in sex ratio of noisy miners associated with bird age (mature/immature), cull number (initial/first recolonisation/second recolonisation) and study region (Bundarra/Fifield). Bold text indicates significant at *P* < 0.05.

Source	d.f.	Chi-square	*P*
Age	1	12.933	**0.0003***
Cull	2	5.362	0.0685
Region	1	0.142	0.7061
Age × Cull	2	2.628	0.2687
Age × Region	1	0.017	0.8977
Cull × Region	2	3.222	0.1997
Age × Cull × Region	2	10.617	**0.0049***

Discussion

Understanding variations in the age and sex ratio of wild populations is extremely challenging because these traits can vary seasonally, annually, according to spatial scale and also between the age and sex classes of a given population (Ellegren and Sheldon 1997). In this study, we detected changes in age and sex structure of wild populations in response to human intervention through removal of resident populations, but the response varied with location and could not be generalised.

Significant male biased sex ratios were observed in both study regions in pre-cull populations, but they did not differ from parity in recolonising populations. This equalisation in overall sex ratios appeared to be driven by an influx of immature birds that exhibited an unbiased sex ratio. Superficially, these results confirm our predictions that (1) *recolonised populations will have a significantly higher proportion of females than were present in the original population*, and (2) *recolonised populations will have a significantly higher percentage of immatures than were present in the original population*. However, the swamping of

the overall demographic signal by immature birds concealed a differential response in the adult cohorts between study regions, which contradicts the mechanisms we proposed to explain these predictions. Specifically, while one population exhibited a significant reduction in male bias in the final population, the other exhibited a significant increase in male bias. The two study regions differed in several fundamental attributes, and although these attributes are confounded, it is important to consider their possible influence on recolonisation dynamics.

Timing of bird removal and the effect on age structure

Noisy miners breed year round, but most breeding occurs during the more productive months of spring (Higgins *et al.* 2001). Because culling at Bundarra took place in November and December, free flying immature birds were available in the landscape as potential colonists of the newly vacant habitat. This contrasted with the situation at Fifield where the August and September culls occurred prior to the fledging of new season birds. This explains the much younger age structure observed in the initial and first recolonisation samples at Bundarra compared with Fifield. By the following autumn, when the final culls occurred, peak breeding was completed and immature birds were fully represented in both regions.

Juvenile dispersal is typically the dominant dispersal phase for passerine birds (Greenwood and Harvey 1982; Donovan *et al.* 1995) and this is the simplest explanation for the high proportion of juveniles in recolonised populations of noisy miners. While an age structure comprising 65–67% immature birds (as observed in Bundarra first recolonisation and Fifield second recolonisation) strongly suggests recolonisation by disproportionate movement of immatures, the culling intervention did not have the necessary controls to draw this conclusion experimentally – it is conceivable that recolonists were simply a random representation of what was naturally a
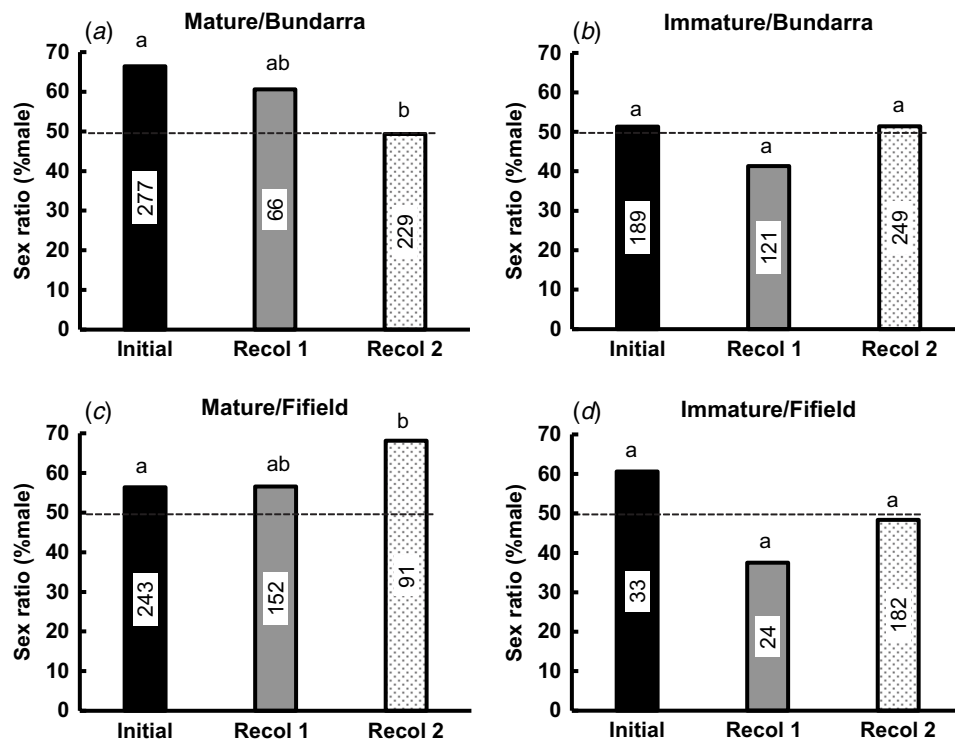
146

Fig. 5. Variation in sex ratio between recolonisation events of (*a*, *c*) mature birds and (*b*, *d*) immature birds. Bars sharing the same letter within histograms are not significantly different (*P* < 0.05). Numbers within the bars indicate sample size. Dotted line shows sex ratio parity. Refer to text for timing of each sample, which varied between regions.

landscape wide young population structure. However, such young age structures are not generally the case among long lived, colonial Australian honeyeaters. The closely related and cooperatively breeding Bell Miner (*M. melanophrys*) provides the strongest comparison and, surveyed over 5 years, it exhibited an annual mean age structure of 20–45% immatures, which fluctuated between seasons (Clarke and Heathcote 1990). This is consistent with the pre-treatment age structures we observed of 41% and 12% immatures, at Bundarra and Fifield, respectively in our study. Moreover, the high percentage of immature birds in the second recolonisation events is likely to be an underestimate, because skull pneumatisation is expected to be complete in 4–8 months (Serventy *et al.* 1967) rendering birds that fledged in early spring unidentifiable as immatures. We are therefore confident that at the time of year when they were present (November–May), immature birds were disproportionately responsible for recolonisation.

Sex ratio of immature birds

Immature recolonists could originate from the surrounding landscape or as new recruits from on-site breeding. While some on site breeding recruitment was probable in the second (autumn) recolonisation event, it was unlikely in the first, because there was insufficient time for recolonists to fledge young in the short period 1 month before the second cull. Irrespective of any on-site breeding that occurred, there was no evidence of immature sex ratios deviating from parity. In both regions and all culls, immature sex ratios reflected the even primary sex ratios normally found in the species prior to the development of the male-bias that arises through the high occurrence of female displacement (Arnold *et al.* 2001; Higgins *et al.* 2001; Barati 2017). While it is unclear at what age female-biased displacement occurs, it is thought to occur as birds approach breeding age and begin to search for breeding positions, which could occur from 8–12 months of age (Higgins *et al.* 2001). This is known to be the situation in the Bell Miner, where the mean age of dispersal is 8 months, close to the minimum observed age of first breeding for both males (8.3 months) and females (9.7 months) (Clarke 1988; Clarke and Heathcote 1990).

In the present study, it seems that both male and female immatures chose to disperse from colonies at an earlier age, and at the same rate. Whilst females usually disperse more often than males due to mother–daughter breeding competition (Clarke and Heathcote 1990), male dispersal may also be substantial. The movement of young males might reflect an optimisation of the queuing strategy,

where young birds seek access to better breeding resources in a new colony than they have in their existing space (Wiley and Rabenold 1984). For example, a reproductive queue forms in superb fairy-wrens (*Malurus cyaneus*) in which males queue to gain a breeding opportunity (Cockburn *et al.* 2008), with some males moving from their natal territory to minimise the wait for a breeding position. Male dispersal may result in greater fitness benefits, than remaining as a philopatric helper, in the absence of ecological constraint (Woolfenden 1989) which, in territorial species, is hypothesised to be the saturation of suitable habitat by sedentary established groups (Koenig 1981; Emlen 1982; Stacey and Ligon 1987). Following thorough removal of noisy miners in our study sites there was a sudden large scale release of productive habitat, and immatures of both sexes from nearby colonies may have perceived a benefit from early dispersal. The perception of vacant habitat could have arisen while performing social activities such as 'long-flights' (Dow 1975), or chasing intruders, and possibly during what would be the short term transient dispersals that act as a precursor to successful permanent dispersal, as seen in other cooperative breeders (Gaston 1978; Lewis 1982; Clarke and Heathcote 1990).

Sex ratio of mature birds

The unchanged sex ratio amongst matures in the first recolonisation event, which was evident in both regions, indicates that mature individuals of both sexes initially moved into suitable vacant habitat in proportion to their original respective abundances. The most likely explanation for this type of recolonisation is that nearby colonies shifted or extended their boundaries to incorporate the newly vacated habitat, rather than movement of subordinate non-breeding floaters (Smith 1978). Recolonisation by floaters that could not previously establish a breeding position appears unlikely because floaters would be expected to be female dominated, given the higher incidence of female displacement (Arnold *et al.* 2001; Higgins *et al.* 2001; Barati 2017).

The disproportionate representation of female colonists in the second recolonisation at Bundarra, resulting in sex-ratio parity among mature birds, is consistent with the female dispersal patterns suggested in this species (Dow 1977, 1978). Females establish activity spaces within a colony and aggressively exclude other female noisy miners from this area. Due to territory spaces being limited within the colony, young female birds are rarely able to establish their own activity space in their natal colony (Dow 1978). This favours females dispersing, while males remain philopatric and contribute to helping behaviour (Barati *et al.* 2018*b*). Females are thus expected to be disproportionately represented in recolonistion of vacant habitat, as observed.

However, the even higher represenation of mature male colonists in the second recolonisation at Fifield, resulting in an even greater male bias, cannot be explained by existing knowledge of this species (Arnold *et al.* 2001; Higgins *et al.* 2001; Barati 2017). Elevated immigration rates of mature males into the vacant habitat could lead to increased male bias, but such dispersal behaviour is inconsistent with previous studies of unmanipulated populations. A plausible mechanism for disproportionate male dispersal in our manipulated populations is that mature male helpers that are queuing for breeding positions may perceive an advantage in emigrating into newly vacant habitat that has been colonised predominantly by immatures. Such an advantage might be accrued from an increased likelihood of finding a mate on account of an even sex-ratio and the inferior competitiveness of less experienced males. However, if valid, this strategy should have been equally profitable in the Bundarra region, where it was not evident. An alternative mechanism is that as they matured, some immature females that had initially recolonised the vacant habitat emigrated a second time, perhaps because the overall density of birds became higher than the original population. Again, this hypothesis is weak, given that the same circumstances occurred at Bundarra but disproportionate male dispersal was not evident.

Drivers of regional variation in recolonisation response

So why were the recolonisation responses in the two regions different? The simplest explanation for differences in sex biased dispersal between regions is regional variation in background sex ratio. Previous studies on undisturbed noisy miner populations have found considerable variation in the magnitude of male bias, range between 2.1:1 and 4.7:1 (Dow 1978; Dow and Whitmore 1990; Arnold *et al.* 2001; Barati *et al.* 2018*a*), with no reports of female biased or sex ratio parity in adult populations. Interestingly, the initial sex ratios we observed of 1.5:1 (Bundarra) and 1.3:1 (Fifield) are the least skewed recorded to date, highlighting the possibility of different sampling biases between 'catch and release', and 'cull and keep' sex determination methods. But regardless of any sampling bias, the similarity of the background sex ratios between study regions does not provide a compelling explanation for the different regional responses we observed in recolonisation demography.

Noisy miner supply in the landscape is another important theoretical driver of recolonisation dynamics, and we had clear evidence of differences between regions. Culling rates were significantly higher in the Bundarra region, most likely reflecting greater noisy miner densities, although we cannot exclude the possibility that the more extensive landscape vegetation cover at Bundara (Fig. 1) facilitated dispersal across the agricultural landscape, increasing mid-cull recolonisation. This difference in landscape supply is also likely to be related to productivity (Montague-Drake *et al.* 2011), with Fifield situated closer to the western edge of the species' range (Fig. 1.) and receiving lower rainfall

than Bundarra (Fig. 2.). Regardless of the cause of the greater culling rate of noisy miners in Bundarra, elevated supply could conceivably explain the more frequent dispersal of females given that it should increase competition, and female/female competition is thought to drive female dispersal (Clarke and Heathcote 1990). In the more challenging environment of Fifield, it seems that larger groups or even coteries of miners move as a unit to recolonise an area. This may be due to better quality habitat being available elsewhere for coteries living in sub-optimal habitat within existing colonies, for example. Under this scenario, increased male sex ratio bias in the second recolonisation episode at Fifield, relative to pre-culling levels, may reflect larger groups of (predominately male) birds emigrating along with dispersing females to better quality habitat. Molecular analysis is required to unravel some of these more elaborative interactions between factors or other as yet unidentified variables that are driving the current patterns observed.

Conclusion

The detrimental impact of the noisy miner's hyper-aggression on Australia's woodland avifauna is recognised in multiple Key Threatening Process listings (NSWSC 2013; TSSC 2013). While habitat restoration is the most favoured recovery action, culling is potentially a rapid and cost effective method of releasing suitable habitat for woodland birds. Culling has produced an enduring benefit in some situations with negligible recolonisation over several years (Grey *et al.* 1997), but in other situations, such as the experiment producing the birds analysed in the present study, recolonisation has been rapid (Davitt *et al.* 2018). A recent meta-analysis of culling trials (Melton *et al.* 2021) was unable to explain the success or failure of culls in terms of noisy miner recolonisation, but a common observation amongst trials was the recovery of small birds, even in situations where noisy miners recolonised quickly. Our study helps explain both the variability in recolonisation response of noisy miners, and the recovery of small birds in the face of noisy miner recolonisation.

The timing of a cull is likely to influence its impact because the source of colonists varies strongly with season. Post-spring culls should primarily result in recolonisation by immature birds, most likely small groups moving in from different colonies. These recolonists would not have established social structures, which would be unlikely to form until after the following breeding season, because the majority of helping behaviour is provided by adult males that are close genetic relatives of the breeders – primarily retained offspring (Barati *et al.* 2018a). Given that the hyper-aggression of noisy miners is related to their strong co-operative behaviour, small birds dispersing into habitat recolonised by unstructured immature noisy miners are less likely to be excluded than

in habitat where aggression is co-ordinated. This provides a plausible mechanism for the observation that small birds often show positive responses to noisy miner removal, even when sites are rapidly recolonised.

Similarly, decreased aggression and positive small bird response are expected in situations where the post-cull sex ratio becomes less male biased (e.g. Bundarra), because male birds contribute more than females to group mobbing behaviour and colony defence (Higgins *et al.* 2001). The information here is not sufficient to explore these impacts in a quantitative manner, but the timing of culls and the sex ratio of recolonists are clearly of ecological importance and must be considered in further experimental removals to refine noisy miner management practices. To this end it would be very instructive if regional removals involving multiple sites were implemented such that replicated randomised sites were sampled in different seasons. It would also be instructive to use genetic techniques to determine comparative levels of relatedness among colonists to determine their likely sources.

Supplementary material

Supplementary material is available online.

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