



Breeding biology of Crimson Finches (*Neochmia phaeton*) in the eastern Kimberley, Western Australia

Catherine Mary Young, Kristal Elaine Cain, Nina Svedin, Patricia Ruth Yvonne Backwell & Sarah Rosalind Pryke

To cite this article: Catherine Mary Young, Kristal Elaine Cain, Nina Svedin, Patricia Ruth Yvonne Backwell & Sarah Rosalind Pryke (2019) Breeding biology of Crimson Finches (*Neochmia phaeton*) in the eastern Kimberley, Western Australia, *Emu - Austral Ornithology*, 119:2, 106-115, DOI: [10.1080/01584197.2018.1549951](https://doi.org/10.1080/01584197.2018.1549951)

To link to this article: <https://doi.org/10.1080/01584197.2018.1549951>



Published online: 05 Dec 2018.



Submit your article to this journal [↗](#)



Article views: 99



View related articles [↗](#)



View Crossmark data [↗](#)



Breeding biology of Crimson Finches (*Neochmia phaeton*) in the eastern Kimberley, Western Australia

Catherine Mary Young , Kristal Elaine Cain, Nina Svedin, Patricia Ruth Yvonne Backwell and Sarah Rosalind Pryke

Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, Australia

ABSTRACT

Many species show pronounced differences in life-history traits, from the individual level to divergences between distinct populations. Understanding the variation in these traits provides not only an insight into individual fitness but also essential information for the management of wild populations. Despite their popularity in aviculture and importance for captive research, our knowledge of many Estrildid finches in the wild is limited. Here we detail the breeding behaviour of 12 discrete colonies of Crimson Finch (*Neochmia phaeton*) in the east Kimberley region of Western Australia over two breeding seasons, and contrast our findings with studies on populations occupying different habitats. We found that many aspects of Crimson Finch breeding biology were consistent across site and studies. However, in our populations, adult survival was lower and group sizes were larger than has been reported elsewhere. We also examined age and sex differences in nestling care and found weak support for age or sex differences in feeding rates. We briefly discuss these findings in relation to theories of colony formation. These findings may help explain the evolution of colonial breeding in this species, as well as having implications for long-term ecosystem management.

ARTICLE HISTORY

Received 3 April 2018
Accepted 14 November 2018

KEYWORDS

Crimson Finch; Estrildid; breeding; colonial; tropical birds

Introduction

In order to ensure the long-term survival of species in the face of ecological threats such as altered fire regimes, climate change, and landscape fragmentation, it is important that we have an understanding of their biology in the wild. In particular, an in-depth knowledge of breeding systems can help us predict how populations might respond to these threats and ultimately have a direct influence on future management plans. However, species often show substantial variation in basic biology at different scales, from among individuals in a population to between populations across a species range (Lambrechts *et al.* 1997). Investigating natural variation between populations enables us to examine the factors that influence the fitness consequences of life-history and behavioural decisions. This approach can lead to critical insights into adaptive life-history traits that are closely linked with fitness (e.g. Lambrechts *et al.* 1997; Blondel *et al.* 1999).

Finches of the family Estrildidae, otherwise known as grassfinches, are widespread across the Australasian region, including the tropics, Tasmania, and in the arid zone (Forshaw and Shephard 2012). Despite this wide distribution, for many grassfinch species, most of our knowledge comes from aviculture where birds have

been selectively bred in captivity and provided with ample resources for many generations. The Zebra Finch (*Taeniopygia guttata*) in particular has rapidly become the most important captive model passerine system (Griffith and Buchanan 2010). However, captive observations may not accurately represent how birds behave in a natural setting, and data on the behaviour of Estrildidae species in the wild remain limited. For example, the few studies that have investigated provisioning rates (as a measure of parental care) in granivorous species have focused primarily on captive populations (e.g. Zebra Finches; Lemon and Barth 1992; Royle *et al.* 2006). However, Gilby *et al.* (2011) found that nest provisioning rates were much higher in captive compared to wild Zebra Finches. This suggests that relying solely on captive populations for life-history data can be misleading and that studies on wild populations are essential. In addition, behaviour may show pronounced differences across populations, but for many species our knowledge of their behaviour in the wild is restricted to a single study site.

Crimson Finches (*Neochmia phaeton*) are an Estrildid grassfinch native to northern Australia. They are a good example of how relying on observations in captivity can lead to an incomplete picture of a species

life-history. For example, Crimson Finch males are known to be highly aggressive and in captivity are often housed in pairs, yet in the wild they are considered highly social, living year-round in colonies (Higgins *et al.* 2006). This aggressive streak means they are difficult to breed in captivity (Forshaw and Shephard 2012). Furthermore, in the wild, Crimson Finches are known to be habitat specialists requiring areas with *Pandanus* trees, tall seeding grasses such as *Chionachne cyathopoda* and fresh surface water (Higgins *et al.* 2006; Dorricott and Garnett 2006; Milenkaya *et al.* 2011; Houston and Black 2014), circumstances difficult to replicate in captivity. It is possible that Crimson Finch habitat preferences could be important in explaining the apparent contradictory pattern of aggression and their penchant for colony life, but this has not yet been explored.

Species that are habitat specialists, especially those that are sedentary, are particularly vulnerable to landscape modifications such as habitat degradation from increased grazing pressure and changes to fire regimes (Keinath *et al.* 2017). Crimson Finches are no exception and have experienced a substantial reduction in range over the last century (Houston and Black 2016). Without a thorough understanding of the ecology and habitat requirements of any species, it is extremely difficult to account for population declines, and to mitigate further range reductions. Here we describe the breeding ecology of a population of free-living Crimson Finches in the eastern Kimberley region of Western Australia. We consider population dynamics and colony size, reproduction, parental care, adult morphology and the relationship between colony size and the extent of their preferred breeding habitat (*Pandanus*). Additionally, we provide comparisons with other populations of Crimson Finches from data presented by Todd (2002) and Milenkaya *et al.* (2011) to examine the relationship between behaviour, population dynamics and ecology.

Methods

Study species

Crimson Finches occur across the tropical savannahs of northern Australia (Figure 1(a)). The nominate subspecies (*N. p. phaeton* or Black-bellied Crimson Finch) spans Western Australia, the Northern Territory and Queensland, while the subspecies (*N. p. evangelinae* or White-bellied Crimson Finch) is confined to Cape York and is listed as threatened (Figure 1(a)). They are considered sedentary, with small local movements; long-distance dispersal is considered difficult because

of their small wing/body-length ratio compared to other species of finches (Higgins *et al.* 2006). Crimson Finches exhibit sexually dimorphic plumage, with the sexes easily distinguished in the field, and also show age-related plumage differences until after their first breeding season (Milenkaya *et al.* 2011). As with other Australasian finches, Crimson Finches are primarily granivores, although a relatively high proportion of their diet also consists of insects (Todd *et al.* 2003).

Study area

We monitored Crimson Finch groups (nominate race *N. p. phaeton*) between the towns of Wyndham (15.49° S, 128.12°E) and Kununurra (15.77°S, 128.74°E) in north-western Australia over 2 years (2013 and 2014; Figure 1(b)). In this region, the nesting substrate that Crimson Finches prefer, namely *Pandanus spiralis* trees, grows primarily on floodplains close to permanent, open water sources (e.g. rivers or natural springs). This is in contrast with a previous study detailing Crimson Finch breeding, which focused on populations that breed primarily in *Pandanus* growing in a continuous band along rivers (e.g. Milenkaya *et al.* 2011). This clumping of nesting habitat allowed us to monitor discrete colonies of birds.

For this study a colony was defined as all the birds that occurred within a discrete area of *Pandanus* vegetation, isolated by areas of savannah grassland. Breeding typically occurs in the first half of the year, corresponding to the tropical wet season. The timing of breeding has been reported to follow rainfall patterns (Todd 2002; Milenkaya *et al.* 2011; Houston and Black 2014). Daily weather observations were collected from the Australian Bureau of Meteorology (Wyndham, station number 001006 and Kununurra, station number 002656). Fire could have a major impact on Crimson Finch populations; all sites had been affected by dry-season fire in either 2011 or 2012, and six sites were also burnt in August and September 2013.

We quantified preferred breeding habitat by calculating both the size and the density of Crimson Finch preferred nesting habitat, namely *Pandanus* trees. We recorded GPS locations of nesting sites (Garmin etrex20) and used these to create minimum area polygons of nesting habitat coverage (using the Minimum Bounding Geometry tool, ArcGIS 10.1). To measure *Pandanus* density we physically counted the number of live *Pandanus* trees in each area and calculated the number of *Pandanus* divided by area size (from GIS data).

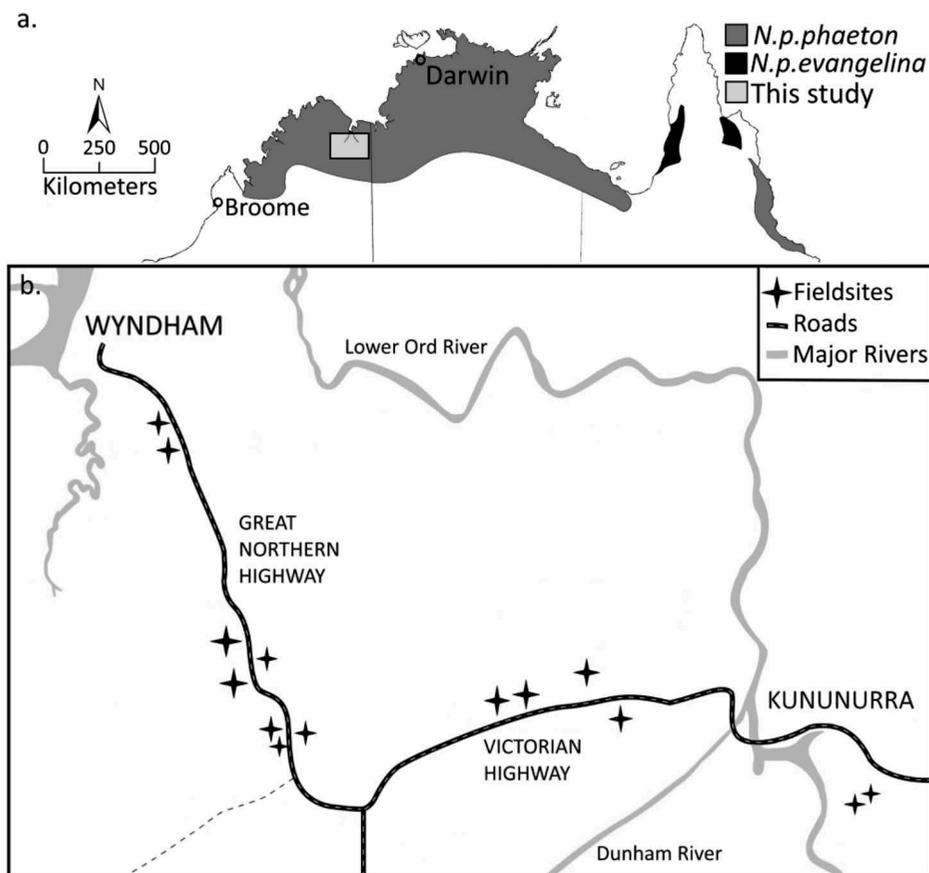


Figure 1. (a) Distribution of Crimson Finches in northern Australia (based on a map in Todd *et al.* 2003). Dark grey areas represent the nominate race *N. p. phaeton* and black areas denote the restricted range of the subspecies *N. p. evangelinae*. The pale grey rectangle represents the site covered in this study, with detail in (b). (b) The study site, a 100 km area between Kununurra and Wyndham in the western Kimberley. A black cross denotes a Crimson Finch colony, with larger crosses denoting larger groups (Figure 1(b) not to scale).

Morphology and population dynamics

From January to May 2013 and January to April 2014 we intensively monitored the breeding of 12 groups, visiting each at least once per week. This allowed for at least five visits to each successful nest. Two additional groups (14 in total) were surveyed for 1 week in the non-breeding season in both years (Figure 1(b)). Adults and juvenile Crimson Finches were caught in mist-nets and banded with individually numbered metal bands from the Australian Bird and Bat Banding Scheme (ABBBS) and a unique combination of three colour bands for individual recognition in the field. At the time of banding we checked for evidence of a brood patch, and measured mass (± 0.01 g), wing chord, maximum tarsus (with the foot at right angles to the tarsus, measured to the intertarsal joint, thus including part of the tibiotarsus), culmen length, and maximum bill depth (± 0.01 mm). Adult birds were aged as either in their first breeding season (2) or older (2+), based on known ages (re-capture data)

and the presence of juvenile primary covert feathers (as described in Milenkaya *et al.* 2011). Group size was calculated from the number of adults caught in a group as well as an estimate of unbanded adults seen at active nests in each area.

Nesting and parental care

We located nests by following birds to their nest sites and searching *Pandanus* trees for active nests. *Pandanus* constitutes the main nesting habitat for Crimson Finches across most of their range (*Pandanus spiralis*; Verbeek *et al.* 1993; Todd 2002; Milenkaya *et al.* 2011). *Pandanus* trees are palm-like structures with long rigid leaves arranged in a spiral pattern and edged with spines. Observations of nest building were made opportunistically while searching for active nests. Nests were monitored regularly for the duration of the nesting period and were considered lost to predation if all of the contents disappeared and the

nest was no longer attended by adult birds (see Young *et al.* 2017 for further details on nest predation). Adults paired assortatively according to age; the majority of pairs being made up of birds of similar age (47 of 71 pairs). Pairs of mixed ages were usually an older male paired with a first-year female (22 of 24 pairs); females were older than their pair male in 2 of 71 nests. Nestlings were banded at approximately 12–14 days old with a numbered ABBBS band and two colour bands. Measurements of tarsus and total head length (± 0.01 mm) and mass (± 0.01 g) were also taken at banding. Brood size was calculated as the number of eggs that hatched; nestlings were aged as days since hatching if known, or age was estimated using size and feather growth. We investigated nestling provisioning rates (feeds/h) by setting up video cameras 4–8 m from nests for 1–4 h at a time, always prior to 9 a.m. Every time a bird entered the nest it was considered a feeding visit except if birds were seen carrying out other duties such as delivering nesting material (feathers or grass).

Analysis and statistics

All statistics were carried out in R (R Development Core Team 2014) using the ‘*lme4*’ package (Bates *et al.* 2014). Variables were first standardised using ‘*arm*’, which centres each variable and divides by two standard deviations (Gelman and Su 2014). Sex differences in morphological measurements (wing, tarsus, bill and mass) were tested for using *t*-tests. All means are presented as mean \pm standard error (SE).

To investigate the factors that might influence feeding rates we used a generalised linear mixed model (GLMM), with feeding rate as the response variable and chick age, brood size, and the age and sex category of adult birds (young male, older male, young female, older female) as predictors. Nest ID was included as a random variable to account for the fact that both males and females from the same nest are included in the same analysis. To select the most parsimonious model we ranked all possible combinations of variables by the Akaike information criterion corrected for small sample size (AICc; Grueber *et al.* 2011), which were obtained using the ‘*AICcmodavg*’ package (Mazerolle

2013). Models with lower AICc values are better supported by the data and only models with $\Delta\text{AICc} < 2$ were retained. Ninety-five per cent confidence intervals (CIs) of estimates of individual predictor variables were used as indicators of each parameter’s importance in each model.

Results

Morphology and population dynamics

In total 400 adults and juveniles and 284 nestlings were banded over the 2 years. On average, males were bigger than females in all measurements (wing, tail, tarsus, bill length and bill depth ($p = < 0.001$)) except mass (Table 1). However, the range of values for males and females almost completely overlapped for all measurements. Colony size ranged from 5 to 74 birds and was higher in 2013 (average 27.8 ± 5.43) than 2014 (19.5 ± 5.67), although not significantly so ($t = 1.14$, $df = 18.20$, $p = 0.27$). Capture rates indicate that the proportion of first-year to older birds varied between years, with groups in 2014 having a higher proportion of younger birds (38% in 2013; 62% in 2014). Of the three colonies in which we are most confident the majority of birds were recorded in both years (that is, colonies with highest capture and observation efforts), just 46 of the 206 adults banded in 2013 were re-sighted in 2014 (22%).

Nesting and parental care

Nests were built exclusively by males with grass and strips of dead *Pandanus*, lined with feathers and commonly containing pieces of snake skin. Females were occasionally seen arranging material delivered by males ($n = 5$) but never directly contributed material. Males continued to make adjustments to nests throughout the nesting period. Nesting commenced in December in both years; nest searching and monitoring began in the first week of January. Nests found at this time often contained eggs but no fledglings were seen until the end of January. The peak of breeding occurred from late January to March (Figure 2), with 82% of nests initiated in this period. We found 56% fewer nests in January–March 2014 (71 nests) than in the same period

Table 1. Sex differences in morphology. Results of *t*-tests comparing morphological measurements (mm) for male and female adults and the average of measurements for males ($n = 141$) and females ($n = 96$), and their standard errors.

	Wing	Tail	Bill length	Bill depth	Tarsus	Mass
Male (\pm SE)	53.4 \pm 0.12	67.7 \pm 0.38	10.6 \pm 0.03	8.0 \pm 0.02	17.6 \pm 0.04	9.6 \pm 0.05
Female (\pm SE)	52.3 \pm 0.15	64.2 \pm 0.40	10.3 \pm 0.03	7.7 \pm 0.03	17.4 \pm 0.06	10.2 \pm 0.09
<i>t</i> -value	−6.82	−6.73	−6.02	−8.00	−2.82	5.41
Sample size (male/female)	141/96	140/94	141/96	141/96	142/96	135/91
<i>p</i> -value	<0.001	<0.001	<0.001	<0.001	0.005	<0.001

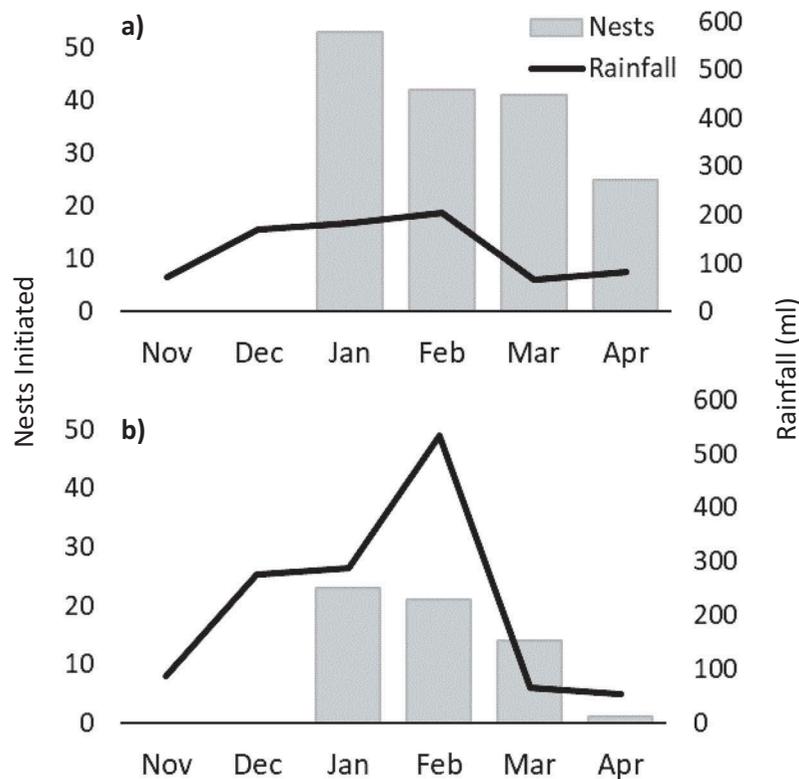


Figure 2. The number of nests initiated each month (left axis, grey bars) with monthly wet season rainfall (right axis, black line) for (a) 2013 and (b) 2014. Nest searching was not undertaken in November and December.

in 2013 (156 nests) despite the same search effort. On average, nest height was 2.20 ± 0.09 m (range 0.5–9 m). Rainfall from November to April (the wet season) was very different for each year; 2013: 696.7 ml and 2014: 1252.9 ml (Australian Bureau of Meteorology).

Clutch sizes ranged from one to seven eggs ($n = 184$), although clutches of seven were found only in 2013. The mean number of eggs per nest was similar between the two years (2013: 5.20 ± 0.17 ; 2014: 5.36 ± 0.09) ($t = 0.80$, $df = 115.75$, $p = 0.42$). Hatching success (in nests where at least one egg hatched) ranged from 33 to 100% but was on average 92% ($n = 96$). Brood size was similar between years (2013: 5.07 ± 0.17 ; 2014: 5.02 ± 0.14) ($t = 0.20$, $df = 83.32$, $p = 0.84$). Of monitored nests where at least one egg was laid ($n = 182$), 34.6% fledged one or more young successfully and daily nest survival was 0.97 (see Young *et al.* 2017). Although males contribute to incubation, only one breeding male developed a brood patch, while more than two-thirds of females caught in the breeding season had a developed brood patch.

On average, parental visits to the nest were made 1.12 ± 0.1 times/h (range 0.34–4.0). As Crimson Finches are granivorous, food items brought to the nest could not be observed. Visitation rate was unrelated to the age of the chicks but was increased with the size of

the brood (Figure 3(b)), as was related to the age and sex of the adult birds (Table 2; $n = 50$). Four models were found to have an $AIC_c < 2$, including the null model, suggesting that support for these effects are weak, but is likely to be influenced by the relatively small sample size. Older males fed more frequently than any other age class, while older females fed least frequently (Figure 3 (b)). Although brood patches were absent for most males, both sexes brooded the young. The average time spent at the nest was 3 min 51 s for females ($n = 56$) and 3 min 56 s for males ($n = 56$).

Habitat and colonial breeding

We assembled information on group size and habitat variables for 12 areas in 2013 and 8 areas in 2014. The area of breeding habitat (*Pandanus* stands) ranged from 0.05 to 22.8 ha, with a mean of $55\,865 \text{ m}^2 \pm 24\,261 \text{ m}^2$. The number of *Pandanus* within a colony ranged from 32 to 5179 (mean 1078 ± 454). The size of the area calculated as breeding habitat using GPS data was related to the number of *Pandanus* trees (Pearson's correlation $r = 0.9$, $df = 10$, p -value = < 0.01). *Pandanus* tree stand density ranged from 0.10 to 0.61 trees per m^2 (mean 0.31 ± 0.05). There was no relationship between group size and *Pandanus* density

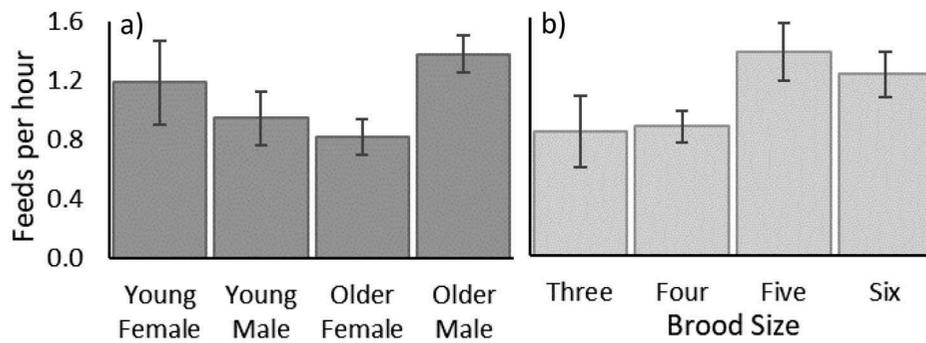


Figure 3. The influence of (a) adult age/sex and (b) brood size on provisioning rates (based on raw data \pm SE).

Table 2. Factors influencing feeding rates at the nest. All models with Δ AICc < 2, investigating factors that may influence feeding rates. All factors tested other than chick age appear in the top models. Factors where the confidence intervals do not cross 0 (indicating importance in the model) are highlighted in bold.

Model	Variable	Estimate \pm SE	AICc	Δ AICc
1	Intercept	0.03 \pm 0.12	97.9	
	Brood size	0.34 \pm 0.21		
	Sex & Age	0.40 \pm 0.24		
2	Intercept	0.04 \pm 0.11	97.1	0.23
	Brood size	0.36 \pm 0.21		
3	Intercept	0.01 \pm 0.13	97.3	0.40
	Sex & Age	0.36 \pm 0.23		
4	Intercept	0.03 \pm 0.12	97.6	0.70

(Pearson's correlation 2013: $r = 0.3$, df 10, $p = 0.5$; 2014: $r = -0.17$, df 6, $p = 0.7$), breeding habitat area (Pearson's correlation 2013: $r = 0.1$, df 10, $p = 0.8$; 2014: $r = 0.4$, df 6, $p = 0.4$), or number of *Pandanus* (Pearson's correlation 2013: $r = 0.3$, df 10, $p = 0.4$; 2014: $r = 0.5$, df 6, $p = 0.2$).

Discussion

We examined how the relationship between colony size and preferred breeding habitat (*Pandanus*) interacts with population dynamics and colony size, reproduction, parental care, adult morphology in the group living Crimson Finch. While some of these factors have previously been investigated in Crimson Finch colonies, our study examines details of breeding ecology in divergent ecological conditions from previous studies (e.g. Todd 2002; Milenkaya *et al.* 2011). We found that some aspects of the breeding biology were stable while other aspects show variability. We also add to the limited number of studies that examine nestling provisioning rates in free-living granivorous species.

Morphology and population dynamics

We found that, on average, males were larger than females, but that the range of the traits measured overlapped completely, which aligns with previous work in other populations of this species (Higgins *et al.* 2006; Milenkaya *et al.* 2011). We found that just 1 of the 152 males of breeding age captured, developed a brood patch. The presence (or absence) of male brood patches is rarely published. However, despite the majority of Estrildid males contributing to incubation, male brood patches are not present in this group. In fact, it has been suggested that a true brood patch is completely absent in all Estrildids (Eisner 1960). The reasons for, and impacts of, a lack of a brood patch on incubation are not clear. Auer *et al.* (2007) found that male Chestnut-vented Tit-Babblers (*Parisoma subcaeruleum*) do not possess a brood patch and incubate eggs at a higher temperature than females. On the other hand, Hill *et al.* (2014) suggested that a brood patch meant female Zebra Finch were better able to respond to changes in incubation demand than their male counterparts. The underlying factors influencing sex differences in brood patch on incubation behaviour are still an open question (but see Kleindorfer *et al.* 1995; Kleindorfer and Hoi 1997).

The number of adults re-sighted between years was low, with just 22% of adults banded in 2013 being re-sighted in 2014. However, adult survival in Crimson Finches in other populations has previously been reported as much higher: 70–96% (Milenkaya *et al.* 2011). In that study, apparent adult survival was estimated over a longer period using survival models. Although our re-sighting estimate is not directly comparable with this study, it is unmistakably lower. This difference in survival estimates may be a function of the lower rainfall in 2013 leading to low survival over the dry season when food is already limited, or a reflection of the denser and wetter habitat occupied

by the population studied by Milenkaya *et al.* (2011). Our estimates are more on a par with that reported for Zebra Finches, where the annual adult survival has been reported at 21% between years (Yom-Tov *et al.* 1992). Due to the low adult survival between the two years, and high number of nests in 2013, the proportion of first-year breeders in the population was more than 20% higher in 2014. This occurred despite overall group sizes being lower in the same year and reflects the high number of nests found in 2013.

Nesting and parental care

The observed nest success rate (34.6%) is comparable to that found in a nearby population (28.8%; Soanes *et al.* 2015) and is also similar to other finches in the region (e.g. Long-tailed Finch, *Poephila acuticauda*, 33%; van Rooij and Griffith 2011). As with Long-tailed and Zebra Finches (Zann 1994; van Rooij and Griffith 2011), Crimson Finch pairs that were successful in fledging any young often succeeded in raising the whole brood (53 of 67 nests; 79%). This suggests that predation and not resource limitation is the main source of nest failure in these species (Young *et al.* 2017).

The peak of breeding (measured as number of nests initiated) in this study corresponds with that recorded by Todd (2002). However, it is slightly earlier than that described for other finches in the same region (Long-tailed finch; van Rooij and Griffith 2011; Gouldian finch; Brazill-Boast *et al.* 2013a), suggesting that these species rely on different grasses seeding at different times as primary food sources during the breeding season. As observed in previous studies, our population's breeding activity tracks rainfall patterns, with most nests initiated around the peak of the wet season (Figure 2; Todd *et al.* 2003; Milenkaya *et al.* 2011).

This link to rainfall patterns can be explained by Crimson Finches' reliance on grass seed as a seasonal resource in the monsoonal tropics (Woinarski and Tidemann 1992). However, contrary to expectations, the year with the highest rainfall (2014) also had the lower number of nests found, correlating with a lower group size for all groups that year. This suggests that low rainfall (as observed in 2013) or the timing of rainfall, may create a lag-effect in food availability. For example, *Sorghum*, a critical food source for breeding Gouldian Finches, requires high rainfall until the end of January. As a result, differences in the timing of rainfall can affect seed yield and ultimately reproductive output (Andrew and Mott 1983; Tidemann *et al.* 1999). Subsequent impacts on adult survival over the dry season may also cause lower group reproductive effort in the

breeding season. Addressing this question requires a more detailed study of diet and long-term monitoring of breeding and seasonal changes.

The majority of studies investigating provisioning as a measure of parental care focus on insectivorous species, with very few reports for granivores (Stoehr *et al.* 2001). Feeding rates for Crimson Finches have not been reported previously. Our results ($1.12 \pm 0.1/h$) are comparable to those reported for wild Gouldian Finches ($1.0 \pm 0.09/h$; Brazill-Boast *et al.* 2013b), but higher than those reported for wild Zebra Finches ($0.8 \pm 0.07/h$; Gilby *et al.* 2011). We found no relationship between chick age and feeding rate, as is often found in studies investigating provisioning at the nest. It is possible that sample size was too small and variation too great to pick up an effect. However, previous studies on granivores have also failed to find an influence of chick age on feeding rates (e.g. House Sparrows; Ringsby *et al.* 2009). This may be because granivores carry food in their crops, so the amount can vary greatly and cannot be assessed from a distance (Gilby *et al.* 2011). It is possible that the amount of food delivered may differ more with chick age than provisioning rates, as smaller chicks also have smaller crops. We did find a trend suggesting that broods of five and six nestlings were fed more frequently than those of three and four. This suggests that Crimson Finches are sensitive to the needs of their brood and can adjust their behaviour accordingly.

Although considerable research has been dedicated to reproductive effort in relation to age and sex of breeding birds (such as timing of breeding, reproductive success, foraging skills), very little attention has been given to the influence of these demographics on parental care (McGraw *et al.* 2001), and the limited data show mixed results (McGraw *et al.* 2001; Mariette and Griffith 2012). We found a trend indicating that older males (those in their second breeding season or beyond) fed at a higher rate than any other age/sex category, while older females fed at the lowest rate. Life-history theory predicts that investment will increase with age, as survival and probability of future reproduction decrease (Stearns 1992). Our findings are congruent with this theory for male provisioning, but not for females. McGraw *et al.* (2001) suggest an alternative theory in which males may be sensitive to the provisioning rates of their partners. Female provisioning rates may be condition dependent, with younger females providing food at higher (although also highly variable) rates. Alternatively, adult females may make fewer visits to the nest but deliver more food per trip than their male counterparts.

Habitat and colonial breeding

Colonial breeding is often associated with benefits resulting from aggregation, such as reduced predation risk. Immelmann (1982) described Crimson Finches as the least social of all Australian grassfinches, while simultaneously noting that they breed colonially throughout their range. These seemingly contradictory statements may simply reflect the fact that Crimson Finches aggregate due to habitat preferences, rather than as a consequence of the benefits of group living. Groups of Crimson Finches in this study were stable in terms of size and membership throughout the wet and dry seasons; birds only dispersed as juveniles, before their first breeding attempt (Young *et al.* in prep.). Our group sizes are much larger than those reported previously by Milenkaya *et al.* (2011), Higgins *et al.* (2006) and Houston and Black (2016), who described groups of up to 20 birds. This is likely to be driven by differences in habitat type. In our population, a colony was defined as being all birds that occurred within a discrete area of *Pandanus* vegetation separated from the next patch by uninhabitable habitat (open savannah), whereas previous studies have occurred in more continuous habitat and are likely to have defined groups as feeding flocks. For example, the population monitored by Milenkaya *et al.* (2011) occupies the narrow riparian zone and so forms one long population within which birds may form smaller groups. Additionally, within the Milenkaya *et al.* (2011) population, birds nested very closely together, <1 m in some cases. In our population, the average distance between nests was 20 m (Young *et al.* 2017), creating a very different social dynamic and is likely to make defining a group more difficult. These differences between populations in habitat use can help us understand the evolution and maintenance of colonial breeding in birds. We found that group size was not linked to the size or density of the available breeding habitat, suggesting that, in this part of their range, breeding habitat is not a limiting factor for group size. Rather, we suggest that, in other populations, Crimson Finches are forced to breed in close proximity to one another because of their combined habitat requirements (*Pandanus*, surface water and rank grasses). Finally, despite their colonial breeding, we observed no instances of allopreening or other pair-bonding behaviour, with all social interactions witnessed being aggressive or sexual in nature (displacement, chasing, pecking, grappling, or courting).

Conclusion

The influence of ecology on breeding behaviour and population dynamics is a fundamental question in behavioural ecology. However, to date, many studies

of free-living birds have been based solely on reports from single study sites. Our results suggest that repeating such studies in a variety of habitats can reveal which aspects of breeding biology are species typical, and which are plastic responses to variation in ecology. These differences can potentially help explain the evolution of colonial breeding and have potential implications for species ecosystem management plans. Further, our results point to a continued need to gather data on the breeding behaviour of species in the field. Studies based on captive individuals, particularly in a breeding context, are too often an inaccurate reflection of behaviour seen in the wild. Quality data on breeding behaviour, and the influence of ecology on population dynamics, are critical for making informed management decisions in the face of changing environments and declining populations.

Acknowledgements

This work was supported by Australian Research Council grants (S.R.P.), an Australian National University Ph.D. scholarship (C.M.Y.) and a Fund for Avian Research grant from the Australian Bird Study Association (C.M.Y.). All work was approved by the Australian National University's Animal Ethics Committee (A2012/55). We thank Fiona Finch and Sophie Keats for help in the field as well as Save the Gouldian Fund for providing access to their field station. We are grateful to Thomas Merkling and Liam Bailey for assistance with R software as well as David Hamilton and Louise Young for comments and Isabela Burgher for GIS assistance. We thank the reviewers for their thoughtful and constructive comments on the original manuscript.

Funding

This work was supported by Australian Research Council grants (S.R.P.); an Australian National University Ph.D. scholarship (C.M.Y.); and the Australian Bird Study Association (C.M.Y.).

ORCID

Catherine Mary Young  <http://orcid.org/0000-0002-5983-1138>

References

- Andrew, M. H., and Mott, J. J. (1983). Annuals with transient seed banks: The population biology of indigenous *Sorghum* species of tropical north-west Australia. *Australian Journal of Ecology* 8, 265–276. doi:10.1111/j.1442-9993.1983.tb01324.x
- Auer, S. K., Bassar, R. D., and Martin, T. E. (2007). Biparental incubation in the Chestnut-vented Tit-babbler *Parisoma subcaeruleum*: Mates devote equal time, but

- males keep eggs warmer. *Journal of Avian Biology* **38**, 278–283. doi:10.1111/j.2007.0908-8857.04092.x
- Bates, D., Maechler, M., Bolker, B., and Walker, S. (2014). 'lme4: Linear Mixed-Effects Models Using Eigen and S4'. R Package Version 1.1-7.
- Blondel, J., Dias, P. C., Perret, P., Maistre, M., and Lambrechts, M. M. (1999). Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. *Science* **285**, 1399–1402. doi:10.1126/science.285.5432.1399
- Brazill-Boast, J., Griffith, S. C., and Pryke, S. R. (2013b). Morph-dependent resource acquisition and fitness in a polymorphic bird. *Evolution and Ecology* **27**, 1189–1198. doi:10.1007/s10682-013-9651-1
- Brazill-Boast, J., Pryke, S. R., and Griffith, S. C. (2013a). Provisioning habitat with custom-designed nest-boxes increases reproductive success in an endangered finch. *Austral Ecology* **38**, 405–412. doi:10.1111/aec.2013.38.issue-4
- Dorricott, K. E., and Garnett, S. T. (2006). National recovery plan for the white bellied subspecies of the crimson finch *Neochmia phaeton evangelinae* and the Northern subspecies of the star finch *Neochmia ruficauda clarescens*. Report to the Australian Government Department of the Environment and Water Resources, Canberra. Queensland Parks and Wildlife Service, Brisbane, Australia.
- Eisner, E. (1960). The relationship of hormones to the reproductive behaviour of birds referring especially to parental behaviour. *Animal Behaviour* **8**, 155–179. doi:10.1016/0003-3472(60)90023-3
- Forshaw, J. M., and Shephard, M. (2012). 'Grassfinches of Australia.' (CSIRO Publishing: Melbourne, Australia.)
- Gelman, A., and Su, Y. S. (2014). 'arm: Data analysis using regression and multilevel hierarchical models. R Version 1.7-07.' Available at <http://CRAN.R-project.org/package=arm>
- Gilby, A. J., Mainwaring, M. C., Rollins, L. A., and Griffith, S. C. (2011). Parental care in wild and captive zebra finches: Measuring food delivery to quantify parental effort. *Animal Behaviour* **81**, 289–295. doi:10.1016/j.anbehav.2010.10.020
- Griffith, S. C., and Buchanan, K. L. (2010). The zebra finch: the ultimate Australian supermodel. *Emu*, **110**, v-xii. doi:10.1071/MUv110n3_ED
- Grueber, C. E., Nakagawa, S., Laws, R. J., and Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology* **24**, 699–711. doi:10.1111/j.1420-9101.2010.02210.x
- Higgins, P. J., Peter, J. M., and Cowling, S. J. (2006). 'Handbook of Australian, New Zealand and Antarctic Birds. Vol. 7: Boatbill to Starlings'. (Oxford University Press: Melbourne, Australia.)
- Hill, D. L., Lindström, J., McCafferty, D. J., and Nager, R. G. (2014). Female but not male zebra finches adjust heat output in response to increased incubation demand. *Journal of Experimental Biology* **217**, 1326–1332. doi:10.1242/jeb.095323
- Houston, W. A., and Black, R. L. (2014). Effect of a major flood on breeding and habitat of the Crimson Finch (*Neochmia phaeton*): A riparian specialist. *River Research and Applications* **30**, 609–616. doi:10.1002/rra.v30.5
- Houston, W. A., and Black, R. L. (2016). Grassfinch decline and local extinction of the Crimson Finch *Neochmia phaeton* in the Fitzroy River Basin, Queensland. *Australian Field Ornithology* **33**, 133–142. doi:10.20938/af
- Immelmann, K. (1982). 'Australian Finches in Bush and Aviary.' (Angus and Robertson Publishers: London, UK.)
- Keinath, D. A., Doak, D. F., Hodges, K. E., Prugh, L. R., Fagan, W., Sekercioglu, C. H., Buchart, S. H. et al. (2017). A global analysis of traits predicting species sensitivity to habitat fragmentation. *Global Ecology and Biogeography* **26**, 115–127. doi:10.1111/geb.12509
- Kleindorfer, S., Fessl, B., and Hoi, H. (1995). More is not always better: Male incubation in two *Acrocephalus* warblers. *Behaviour* **132**, 607–625. doi:10.1163/156853995X00234
- Kleindorfer, S., and Hoi, H. (1997). Nest predation avoidance: An alternative explanation for male incubation in *Acrocephalus melanopogon*. *Ethology* **103**, 619–631. doi:10.1111/j.1439-0310.1997.tb00173.x
- Lambrechts, M. M., Blondel, J., Hurtrez-Bousses, S., Maistre, M., and Perret, P. (1997). Adaptive inter-population differences in blue tit life-history traits on Corsica. *Evolutionary Ecology* **11**, 599–612. doi:10.1007/s10682-997-1515-0
- Lemon, W. C., and Barth, R. H. (1992). The effects of feeding rate on reproductive success in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour* **44**, 851–857. doi:10.1016/S0003-3472(05)80581-0
- Mariette, M. M., and Griffith, S. C. (2012). Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch, *Taeniopygia guttata*. *Journal of Avian Biology* **43**, 131–140. doi:10.1111/j.1600-048X.2012.05555.x
- Mazerolle, M. J. (2013). 'AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.35.' Available at <http://CRAN.R-project.org/package=AICcmodavg>
- McGraw, K. J., Nolan, P. M., Stoehr, A. M., and Hill, G. E. (2001). Intersexual differences in age-specific parental effort in the house finch (*Carpodacus mexicanus*). *Etologia* **9**, 35–41.
- Milenkaya, O., Legge, S., and Walters, J. R. (2011). Breeding biology and life-history traits of an Australasian tropical granivore, the Crimson Finch (*Neochmia phaeton*). *Emu* **111**, 312–320. doi:10.1071/MU10088
- R Development Core Team. (2014). 'R: A Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna, Austria.)
- Ringsby, T. H., Berge, T., Saether, B.-E., and Jensen, H. (2009). Reproductive success and individual variation in feeding frequency of House Sparrows (*Passer domesticus*). *Journal of Ornithology* **150**, 469–481. doi:10.1007/s10336-008-0365-z
- Royle, N. J., Hartley, I. R., and Parker, G. A. (2006). Consequences of biparental care for begging and growth in zebra finches, *Taeniopygia guttata*. *Animal Behaviour* **72**, 123–130. doi:10.1016/j.anbehav.2005.09.023
- Soanes, R., Peters, A., Delhey, K., and Doody, J. S. (2015). The influence of nest site choice and predator sensory cues on nest success in the Crimson Finch, *Neochmia phaeton*. *Emu* **115**, 317–325. doi:10.1071/MU14046
- Stearns, S. C. (1992). 'The Evolution of Life Histories.' (Oxford University Press: Oxford, UK.)
- Stoehr, A. M., McGraw, K. J., Nolan, P. M., and Hill, G. E. (2001). Parental care in relation to brood size in the house finch. *Journal of Field Ornithology* **72**, 412–418. doi:10.1648/0273-8570-72.3.412
- Tidemann, S. C., Lawson, C., Elvish, R., Boyden, J., and Elvish, J. (1999). Breeding biology of the Gouldian Finch *Erythrura gouldiae*, an endangered Finch of Northern Australia. *Emu* **99**, 191–199. doi:10.1071/MU99022

- Todd, M. K. (2002). Nest-site and breeding-season data for the Crimson Finch *Neochmia phaeton* in Australia. *Australian Bird Watcher* **19**, 161–171.
- Todd, M. K., Felton, A., and Garnett, S. T. (2003). Morphological and dietary differences between common and uncommon subspecies of Crimson Finch, *Neochmia phaeton*, and Star Finch, *Neochmia ruficauda*, in northern Australia. *Emu* **103**, 141–148. doi:10.1071/MU02015
- van Rooij, E. P., and Griffith, S. C. (2011). Breeding ecology of an Australian estrildid, the Long-tailed Finch (*Poephila acuticauda*). *Emu* **111**, 297–303. doi:10.1071/MU10092
- Verbeek, N. A. M., Braithwaite, R. W., and Boasson, R. (1993). The importance of *Pandanus spiralis* to bird. *Emu* **93**, 53–58. doi:10.1071/MU9930053
- Woinarski, J. C. Z., and Tidemann, S. (1992). Survivorship and some population parameters for the endangered Gouldian Finch *Erythrura gouldiae* and two other finch species at two sites in tropical northern Australia. *Emu* **92**, 33–38. doi:10.1071/MU9920033
- Yom-Tov, Y., McCleery, R., and Purchase, D. (1992). The survival rate of Australian passerines. *Ibis* **134**, 374–379. doi:10.1111/j.1474-919X.1992.tb08017.x
- Young, C. M., Cain, K. E., Svedin, N. S., Backwell, P. R. Y., and Pryke, S. R. (2017). Nesting success in crimson finches: Chance or choice? *Ethology* **123**, 41–50. doi:10.1111/eth.12422
- Zann, R. (1994). Reproduction in a Zebra Finch colony in south-eastern Australia: The significance of monogamy, precocial breeding and multiple broods in a highly mobile species. *Emu* **94**, 285–299. doi:10.1071/MU9940285