
Breeding ecology and ornamentation in the Long-tailed Finch



Erica P. van Rooij

Department of Biological Sciences
Brain, Behaviour and Evolution
Macquarie University
Sydney, Australia

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On the whole, birds appear to be the most aesthetic of all animals...
and they have nearly the same taste for the beautiful as we have.

Charles Darwin

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Abstract

The Long-tailed Finch (*Poephila acuticauda*) is an endemic Australian grassfinch (Estrildid) inhabiting the tropical northern savanna of Australia. Ecologically it is very similar to the well-studied Zebra Finch (*Taeniopygia guttata*) and the endangered Gouldian Finch (*Erythrura gouldiae*) - sharing the same geographic range, but yet has not declined.

Here, in the first extensive field study of the breeding ecology and behaviour of this species, I describe the general breeding ecology of the Long-tailed Finch including mate and site fidelity while drawing a comparison with the zebra finch, and also describe the first observation of cooperative breeding ever recorded for this species.

The Long-tailed Finch possesses several putative ornaments in both sexes including elongated tail streamers, a black throat patch and variation in bill colour. In this study I show that this species is slightly dimorphic in expression of ornamentation thereby removing evidence for the sexual indistinguishability theory. As pairs did not mate assortatively based on ornament expression, mate choice in this wild population did not seem to be based on ornament expression and ornament expression did not seem to signal reproductive success in males or females. This species has low levels of extra-pair paternity, but choice for extra-pair mates does not seem to be based on ornament expression or improve offspring quality. Parental nest visit synchrony is high in this species and has a limited effect on breeding success. Further, parental ornamentation does not signal parental quality and does not affect nestling growth.

The mutual multiple ‘ornaments’ in this species therefore do not currently seem to be under sexual selection, but might play an important role in species recognition.

Statement of Candidate

I certify that the work in this thesis entitled 'Breeding ecology and ornamentation in the Long-tailed Finch' has not been previously submitted for a degree nor has been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged. The contribution of co-authors on published chapters and any assistance received in collection of data and production of the thesis is outlined in the acknowledgement section of each chapter. The research presented in this thesis was approved by Macquarie University Animal Ethics Committee (No. 2007/038).

As each paper is prepared for submission as a stand-alone paper the contributions of co-authors is outlined below. As principal author on all published work my contribution to each thesis chapter can be summarized as follows:

Chapter 1. Conception 100%, writing 100%

Chapter 2. Conception 90%, data collection 90%, analysis 100%, writing 95%

Chapter 3. Conception 90%, data collection 100%, analysis 100%, writing 95%

Chapter 4. Conception 85%, data collection 95%, analysis 95%, writing 90%

Chapter 5. Conception 90%, data collection 90%, analysis 90%, writing 95%

Chapter 6. Conception 90%, data collection 95%, analysis 90%, writing 90%

Chapter 7. Conception 85%, data collection 90%, analysis 95%, writing 90%

Chapter 8. Conception 90%, data collection 100%, analysis 90%, writing 90%

Chapter 9. Conception 100%, writing 100%

Specific contributions of joint authors

Dr. Simon Griffith as supervisor of this thesis has contributed to the concept and design of field data collection. He has also contributed to the statistical analysis and writing of all chapters through advice and improvements to written work.

Clare Holleley was involved in the genetic analysis of blood samples for chapter 6.

Chapter 2, 3, 4 and 5 have been through the process of peer review and were improved on the basis of comments of reviewers and associate editors.

In addition, I certify that all information sources and literature used are properly referenced in the thesis.

A handwritten signature in black ink, reading 'EuRooij'.

Erica P van Rooij

(Student ID 41407385)

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CHAPTER ONE

General Introduction



S. Pryke

Our understanding about avian ecology and evolution is based on intensive studies of relatively few model species (e.g. well-studied birds like the great tit, *Parus major*, blue tit *Cyanistes caeruleus*, house sparrow *Passer domesticus* and pied and collared flycatchers *Ficedula hypoleuca* and *F. albicollis*), which have been used because they nest at easily accessed field sites at relatively high density in the northern hemisphere. However, these species represent a very biogeographically limited area (i.e. most of these classic avian model systems are in the Western Palearctic region), do not represent a great amount of all the variation across birds and most occur in one relatively simple form (i.e. there is little variation in house sparrows, or great tits across Europe). There is a need to understand a broader range of species, as well as in more areas and we can learn a lot about evolutionary processes if we try to understand the variation that occurs between multiple similar forms (e.g. Irwin *et al.* 2001). Australia has many avian species that exhibit interesting variation in form geographically. This study aims to start developing an understanding of one of those – the Long-tailed Finch *Poephila acuticauda*, with the first extensive field study of a wild population in northwestern Australia.

The Long-tailed Finch is closely related to the Zebra Finch (*Taeniopygia guttata*), which is one of the most widely used avian models across many disciplines of biology ranging from genetics and neurosciences to sexual selection and social foraging (Griffith & Buchanan 2010). Long-tailed Finches occur as two geographical and morphologically differentiable populations separated by the Kimberley Plateau–Arnhem Land Barrier, which are variably treated as either full, or sub-species (e.g. Keast 1958; Immelmann 1965; Boles 1988; Jennings & Edwards 2005). They differ mainly in bill coloration with the yellow billed form (nominate *acuticauda*) inhabiting the western, and red billed form (subsp *hecki*) in the eastern part of the range (Higgins *et al.* 2006). Both sexes in the Long-tailed Finch also possess multiple putative ornaments: very long central tail feathers and a black throat patch (Figure 1.1). The

species therefore potentially provides an excellent opportunity for studying sexual selection in males and females as well as speciation.

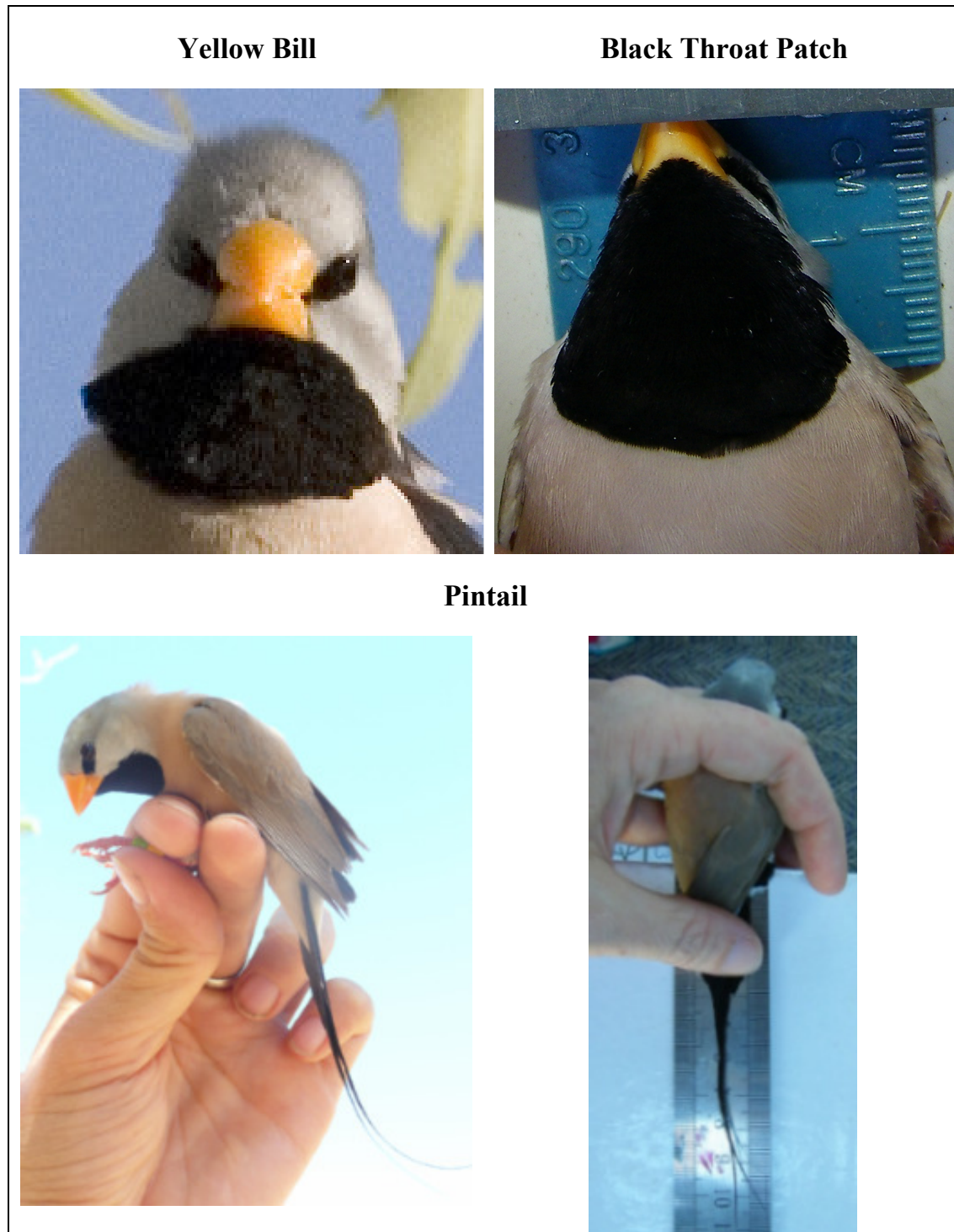


Figure 1.1 Putative ornaments in the Long-tailed Finch

Breeding ecology

To date the breeding ecology of this species has not been reported in great detail by any major study (Higgins *et al.* 2006). The only studies on Long-tailed Finches are in combination with other finches, on nesting sites (Tidemann *et al.* 1992; Brazill-Boast *et al.* 2010) and duration of the breeding season (Tidemann & Woinarski 1994). In a colour-banded breeding population of Long-tailed Finches it will now be possible to study reproductive success and variation in reproductive success between individuals. It will also be possible to assess site and mate fidelity in this species with very close pair bonds (Zann 1977) and draw a comparison to the well-studied zebra finch.

Ornamentation in both sexes

Ornamental secondary sexual traits are widespread throughout the animal kingdom and are well exemplified in birds with many species exhibiting elongated tails, and/or highly coloured plumage or bills whose expression far exceeds any obvious naturally selected purpose (Andersson 1994). The evolution of ornamentation and other secondary sexual characters that are unlikely to contribute to survival was explained by the theory of sexual selection (Darwin 1871). These traits commonly appeared in only males and were thought to have evolved either through intrasexual competition between males to monopolize access to females or through female preferences for mating with superior partners (Darwin 1871).

However, in over half of the world's bird species females appear identical to males (Griffiths *et al.* 1998), but, as yet, these species (Kraaijeveld *et al.* 2007; Clutton-Brock 2007, 2009) have received far less attention than male ornamentation in dimorphic species, where there are clear differences in form, size or colour (Hunt *et al.* 1998). It is not clear why the females in

some species bear traits to the same extent as males (reviewed by Amundsen 2000 and Clutton-Brock 2009), but the mechanisms responsible for the evolution of secondary sexual characters in females are likely to be similar to those operating in males, including intrasexual competition between females, male mating preferences and female competition to attract mates. The Long-tailed Finch is one example of a species where both sexes possess multiple ornaments (Figure 1.1).

Individuals might benefit by being able to conceal their sex, as repeated interactions due to sexual competition would sometimes be disadvantageous (sexual indistinguishability hypothesis Burley 1981), advantages are expected to be greatest in monogamous group living species (Burley 1981). The only rigorous support that sexually monomorphic group-living species are unable to distinguish sex comes from Burley's (1981) study of feral pigeons and a study of the Long-tailed Finch (Langmore & Bennett 1999).

Mutual Mate choice: social and extra-pair mate

Elaborate or extravagant traits in males are assumed to result from intra- or inter sexual selection (Andersson 1994), targeting good quality individuals through condition dependent trait expression (Andersson 1986; Grafen 1990). The existence of ornamental traits expressed in both sexes may be favoured by mutual sexual selection driven by both female and male competition for mates (Darwin 1871; Trail 1990), which has been confirmed in other sexually monomorphic species (e.g. Jones & Hunter 1993; Romero-Pujante *et al.* 2002; Kraaijeveld *et al.* 2004b). If both sexes have the same preferences in mate ornament expression this may result in assortative mating with respect to ornament expression, where although all individuals attempt to gain a mate of the highest quality, those of low quality are competitively constrained in mate choice (Burley 1983; Johnstone *et al.* 1996). Positive

assortative mating can occur by body size (e.g. Johnstone *et al.* 1996; Komdeur *et al.* 2005), but also by ornaments, e.g. bill and plumage colour (Jawor *et al.* 2003), patch size (Masello & Quillfeldt 2003) and other plumage ornaments (e.g. Kraaijeveld *et al.* 2004b).

The level of sexual selection in most socially monogamous birds is largely dependent upon the level of, and distribution of extra-pair paternity (EPP) amongst males in a population. Males can increase the number of offspring they sire by engaging in EPP. However, in mutually ornamented species males could also aim to increase the genetic quality of some of their offspring by selecting a female more attractive than their social mate, a perspective that has not previously been examined. For females, engaging in extra-pair copulations (EPCs) does not increase the number of offspring they produce, but they could base their choice of extra-pair males on the expression of male ornamental traits, which are often viewed as condition-dependent signals of male quality and thereby gain genetic benefits for their offspring (Andersson 1994; Cotton *et al.* 2004). If females and/or males have EPCs to gain genetic benefits for extra-pair offspring this should result in better offspring (e.g. Kempenaers *et al.* 1997; Sheldon *et al.* 1997; Johnsen *et al.* 2000).

Parental care and nestling growth

Parental care is common in birds, with bi-parental care occurring in more than 90% of species (Clutton-Brock 1991). Since each parent's own future potential would be enhanced if the other parent contributed more of the total investment in offspring, there is an interesting conflict between the sexes (e.g. Trivers 1972; Royle *et al.* 2002; McNamara *et al.* 2003). Much of the research into bi-parental care has investigated the sources of variation in the level of care provided by individual males and females, particularly in the context of theoretical ideas such as the good-parent hypothesis (Hoelzer 1989) and the differential allocation

hypothesis (Burley 1988). These hypotheses and much of the work that has followed (e.g. Royle *et al.* 2002) has focused on the different investment strategies of males and females and the potential conflict between the sexes (e.g. Akcay & Roughgarden 2009; Harrison *et al.* 2009; Michler *et al.* 2010; Stodola *et al.* 2010).

Parents can influence their parental care expenditure by creating hatching intervals by determining when to begin incubation (Stoleson & Beisinger 1995), thereby creating size hierarchies within their brood, which is suggested to spread out the food demand of the brood to reduce energy expenditure by the parents (peak load reduction hypothesis; Stoleson & Beisinger 1995). It may also be adaptive if male and female offspring differ in their growth rates to lighten the peak load of the parents, which so far has only been assessed in a few sexually monomorphic species (e.g. Nisbet & Szczys 2001; Becker & Wink 2003; Rosivall *et al.* 2009). Brood size is predicted to have an important effect on nestling growth rate (Godfray & Parker 1992), however because of the costs of reproduction to adults (e.g. Lessells 1986) we might expect females to optimize clutch size to the ability of parents to raise that number of offspring (e.g. Pettifor *et al.* 1988).

In altricial species where the nestlings are entirely dependent on the parents for providing food until fledging - like the Long-tailed Finch - reproductive success is often limited by parental feeding rates (e.g. Royle *et al.* 2006) and nestling development may be affected by parental behaviour. We now have good techniques for recording parental behaviour and measuring and sexing nestlings to try and examine parental nest visit behaviour and nestling growth in more detail.

Study species, study area and field methods

Study Species

The Long-tailed Finch (Poephila acuticauda)

The Long-tailed Finch is a small, socially monogamous passerine of the Estrildid family, endemic to Australia. They are generally regarded as sexually monomorphic in appearance, with both sexes bearing multiple ornaments (Figure 1.2). They form socially monogamous pairs with strong pair bonds (Immelmann 1965; Zann 1977).



Figure 1.2 Pair of Long-tailed Finches (male on the left and female on the right). Photo by C. Mares.

Long-tailed Finches are a gregarious species, occurring in pairs and small family groups during the breeding season, while flocking in search of water towards the end of the dry season (Zann 1977; Higgins *et al.* 2006), often associating with other finches in mixed-species flocks. Their movements are poorly known, but they are thought to be largely sedentary, with little dispersal (Higgins *et al.* 2006; Woinarski & Tidemann 1992). Not much is known about longevity (Higgins *et al.* 2006) with just one study estimating life expectancy to be 16 to 25 months from birth (Woinarski & Tidemann 1992). They are primarily granivorous and mainly eat seeds of several species of native grasses, with the annual *Sorghum* spp. dominant in their diet throughout the breeding season, though they also take invertebrates, mainly insects and their larvae (Dostine & Franklin 2002), particularly during breeding.

Long-tailed finches are facultative cavity nesters and are reported to breed in loose colonies, though usually with only one nest per tree and can raise two or three broods in a season (Immelmann 1965). The reported breeding season for two populations in the Northern Territory runs from early February until September/November and the onset and duration of the breeding season is thought to vary between years in response to variation in the timing and intensity of the wet season rains (Tidemann & Woinarski 1994).

Study Area

The Kimberley Region

Long-tailed Finches are endemic to the savannah woodlands of tropical northern Australia and are abundant and widespread throughout the Kimberley (Evans & Bougher 1987; Figure 1.3). We studied a wild population of Long-tailed Finches in the East Kimberley, around Wyndham, Western Australia.

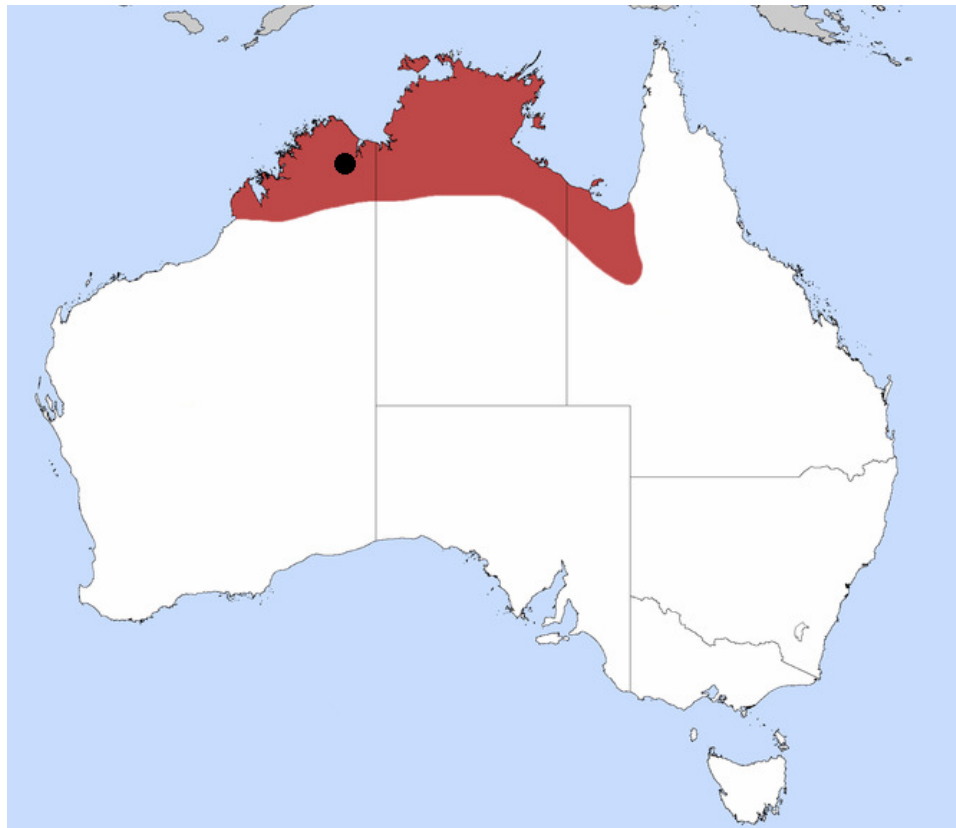


Figure 1.3 Current distribution of the Long-tailed Finch in Australia.

Current distribution of Long-tailed Finches in red; black dot indicating the area where we studied the long-tailed finch population near Wyndham. Source: Wikipedia.

Their main habitat (Figure 1.4) is described as open grassy woodlands and shrub-studded plains adjacent to creeks and watercourses, dominated by eucalypt trees (e.g. *Eucalyptus brevifolia*, *E. dichromophloia*) which are used for nesting and access to water for drinking (Keast 1958, Higgins *et al.* 2006). The field sites were located on adjacent west-facing sandstone ridges and separated by ephemeral creeks (total area ~ 108 ha). The vegetation was characterised as savannah grassland dominated by *Corymbia dichromophloia* (Variable-barked or variegated bloodwood) with some *Eucalyptus miniata* (Darwin woollybutt), with an understory dominated by the grasses *Sorghum stipoides* (Speargrass) and *Triodia bitextura* (Curly spinifex) with some *Panicum decompositum* (Native millet). The area of the site was bordered on one side by intertidal mudflats, with the remaining boundary demarcated by an abrupt change in vegetation (overstorey dominated by non-hollow-bearing species, e.g. *Eucalyptus jensenii*, ironbark).



Figure 1.4 Main habitat of the Long-tailed Finch.

Field methods

We studied the breeding ecology and population dynamics of Long-tailed Finches in the East Kimberley, around Wyndham, Western Australia (15°33'38"S, 128°08'59"E) over three breeding seasons (February to September) in 2008, 2009 and 2010.

Naturally in this area Long-tailed Finches will nest in cavities in *Eucalyptus* trees (Figure 1.5) when they are available or make grass nests constructed in the canopy of these trees (Figure 1.6; Brazill-Boast *et al.* 2010). Following on from a similar approach in the closely related zebra finch (*Taeniopygia guttata*) (Griffith *et al.* 2008), to facilitate the intensive study of the breeding ecology of this species and the Gouldian finch (*Erythrura gouldiae*) in this area we erected about 200 specially designed nestboxes (Figure 1.7; full details in Brazill-Boast *et al.* 2011).



Figure 1.5 Natural nesting cavity



Figure 1.6 Natural free-standing nest

All nest boxes and known cavities in trees were checked for new nesting attempts every six days. Most of the recorded nesting attempts (88%; $n = 377$) however were in nest boxes. Nests were monitored every 2-6 days (depending on the stage of the nest). Nests were

checked daily from two days before the expected hatching date (12 days from the onset of incubation; Higgins *et al.* 2006). At the age of ten days all nestlings were banded, measured and weighed and a small blood sample was taken. All nests were checked just before fledging (age 16 days) and the nestlings present at that time were assumed to fledge.

Adult Long-tailed Finches were caught in mistnets along creeks and with handnets on their nests. All birds were banded with a metal band (supplied by the Australian Bird and Bat Banding Scheme) and a unique combination of three colour bands in order to later visually identify individual birds. Morphological measures were taken of each individual upon catching and sex was determined genetically by analysis of a blood sample. Nestlings were measured every other day from day 2 till day 16 to assess growth rates and banded when 10 or 12 days old. Nests were filmed when nestlings were 10 and 11 days old to assess parental nest visit behaviour, frequency and synchrony (Figure 1.8).



Figure 1.7 Nestbox



Figure 1.8 Nestbox with camera

Camera is positioned on the trunk of the tree (left in the picture)

Thesis outline

This thesis consists of seven chapters plus this introductory chapter and a general discussion.

Chapter 1 (this chapter) gives a general introduction to the thesis and the study species, including this outline and aim. Chapter 2 describes the general breeding ecology and some basic parameters relating to mate and site fidelity in our colour-banded population of Long-tailed Finches. Chapter 3 describes the first observation of the occurrence of cooperative breeding in this species (and indeed in any Australian Estrildid). Chapter 4 aims to determine whether this species is truly monomorphic with respect to morphology, as well as plumage and bill reflectance, by assessing the variation between individuals from a population of wild Long-tailed Finches, asking whether males and females can be reliably distinguished based on morphology. Chapter 5 investigates whether this species mates assortatively based on ornamentation and whether ornaments indicate male and female reproductive success. In chapter 6 we characterise the level of EPP in a population of free-living Long-tailed Finches and investigate the occurrence of EPP in relation with ecological and life-history factors. We also investigated whether morphological characters of males were linked with male success at defending the paternity of the chicks within his own nest and siring offspring in the nests of others and if this resulted in higher quality offspring. Furthermore, we assessed, for the first time, whether males, besides increasing the number of offspring also increased the quality of their extra-pair offspring by selecting a more attractive female as an extra-pair partner. Chapter 7 describes the synchronized parental provisioning behaviour and assesses the effects of parental nest visit rates and visit synchrony on breeding success (e.g. brood size, number of offspring fledged and nestling growth) and whether ornament expression signals parental quality. Chapter 8 investigates nestling growth rates and fledging size and whether these

parameters are affected by nestling sex, brood size and hatching asynchrony. Chapter 9 gives a general discussion and conclusion.

During the course of this research I also contributed towards a paper describing inter-specific interference competition over nest sites between Long-tailed Finches and Gouldian Finches which is included as an appendix because it is useful for introducing the use of nestboxes and the study area.

Aim

This study aims to gain insight in how sexual selection works on a mutually ornamented species with multiple ornaments, but most importantly to initiate the study of sexual selection in a species that has a putative ornamental trait that varies across a cline. The data presented herein expands our understanding of how sexual selection occurs in birds by reporting data on a species on which these questions have not previously been addressed. This study also adds important data to a family that is currently poorly represented in the literature (Estrildid finches) in a region of the world (Australia) in which there have also been relatively few intensive studies of sexual selection in the wild.

CHAPTER TWO

Breeding ecology of the Long-tailed Finch



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2.1 Abstract

The Long-tailed Finch (*Poephila acuticauda*) is a small estrildid finch endemic to Australia's tropical savannah. The breeding ecology of the Long-tailed Finch was studied over three breeding seasons between 2008 and 2010 in the Kimberley, Western Australia. Over this study period, Long-tailed Finches bred from February till September with a peak in egg laying in March / April. Pairs produced up to three successful broods per season with a clutch size of 4.66 ± 1.13 (mean \pm se), brood size of 3.98 ± 1.10 and an average of 3.87 ± 1.10 young fledged per successful nest. Most nesting attempts were in nest boxes. Nest failure rate was high with 66.2% of breeding attempts failing to fledge any offspring. In nests where at least one egg hatched (47% of nests) $87\% \pm 17\%$ of the eggs hatched. In successful nests $98 \pm 9\%$ of all nestlings surviving to fledge successfully. Annual breeding success was relatively consistent over these three breeding seasons with 26.8 – 40.8% of all laid eggs resulting in fledged young.

Successful nesting attempts lasted an average of 39 ± 3.3 days from the date the first egg was laid until the date the young fledged, with both parents contributing to incubation (13.6 ± 2.3 days) and brooding and feeding young during the nestling period (20.6 ± 2 days). Site and mate fidelity were high, with pairs staying together during and between breeding seasons and 60% of pairs breeding in the same area in a subsequent year.

2.2 Introduction

The Long-tailed Finch (*Poephila acuticauda*) is a small grass finch of the estrildid family and endemic to the savannah woodlands of tropical northern Australia. They are abundant and classified as a Least Concern Species (Birdlife International 2009 IUCN red list). They are generally regarded as sexually monomorphic in appearance although a recent study that considered variation in plumage and bill coloration, the size of the black throat patch and length of the tail streamers, found the sexes to be distinguishable from one another (Van Rooij & Griffith 2010). Long-tailed Finches occur as two geographical and morphologically differentiable populations separated by the Kimberley Plateau–Arnhem Land Barrier, which are variably treated as either full, or sub-species (e.g. Keast 1958; Immelmann 1965; Boles 1988; Jennings & Edwards 2005). The two subspecies differ mainly in bill coloration with the orange-yellow billed (nominate *acuticauda*) inhabiting the western part of the range and orange-red to bright red billed (subspecies *hecki*) in the eastern part of the range (Higgins *et al.* 2006).

Their main habitat is described as open grassy woodlands and shrub-studded plains adjacent to creeks and watercourses, dominated by eucalypt trees (e.g. *Eucalyptus brevifolia*, *E. dichromophloia*) which are used for nesting and access to water for drinking (Keast 1958, Higgins *et al.* 2006). They are primarily granivorous and mainly eat seeds of several species of native grasses, with the annual *Sorghum* spp. dominant in their diet throughout the breeding season, though they also take invertebrates, mainly insects and their larvae (Dostine & Franklin 2002).

To date the breeding ecology of this species has not been reported in detail by any major study (Higgins *et al.* 2006). They are reported to breed in loose colonies, though usually with only

one nest per tree and can raise two or three broods in a season (Immelmann 1965). The reported breeding season for two populations in the Northern Territory runs from early February until September/November and the onset and duration of the breeding season is thought to vary between years in response to variation in the timing and intensity of the wet season rains (Tidemann & Woinarski 1994). Long-tailed Finches build enclosed nests in hollows and also build grass nests in the foliage of trees (Tidemann *et al.* 1992; Brazill-Boast *et al.* 2010).

Long-tailed Finches are a gregarious species, occurring in pairs and small family groups during the breeding season, while flocking in search of water towards the end of the dry season (Zann 1977; Higgins *et al.* 2006), often associating with other finches in mixed-species flocks. Their movements are poorly known, but they are thought to be largely sedentary, with little dispersal (Higgins *et al.* 2006; Woinarski & Tidemann 1992). Not much is known about longevity (Higgins *et al.* 2006) with just one study estimating life expectancy to be 16 to 25 months from birth (Woinarski & Tidemann 1992). They form socially monogamous pairs with strong pair bonds (Immelmann 1965; Zann 1977). A recent study reported the first example of cooperative breeding in an estrildid finch, with a mature juvenile remaining with its parents and assisting them to raise the next brood, several months after it was fledged itself (Van Rooij & Griffith 2009).

The aim of this study was to examine the breeding ecology and some basic parameters relating to longevity and dispersal from a colour-banded population of Long-tailed Finches (nominate *acuticauda*) in the Eastern Kimberley of Western Australia.

2.3 Methods

We studied the breeding ecology and population dynamics of Long-tailed Finches in the East Kimberley, around Wyndham, Western Australia (15°33'38"S, 128°08'59"E) over three breeding seasons (February to September) in 2008, 2009 and 2010. The climate at this location is monsoonal, with 80-90% of annual rainfall falling during the five months of the wet season (November to March).

Study site

Study sites were located just south of the town of Wyndham. The field sites were located on adjacent west-facing sandstone ridges and separated by ephemeral creeks (total area ~ 108 ha). The vegetation was characterised as savannah grassland dominated by *Corymbia dichromophloia* (Variable-barked or variegated bloodwood) with some *Eucalyptus miniata* (Darwin woollybutt), with an understory dominated by the grasses *Sorghum stipoides* (Speargrass) and *Triodia bitextura* (Curly spinifex) with some *Panicum decompositum* (Native millet). The area of the site was bordered on one side by intertidal mudflats, with the remaining boundary demarcated by an abrupt change in vegetation (overstorey dominated by non-hollow-bearing species, e.g. *Eucalyptus jensenii*, ironbark).

Naturally in this area Long-tailed Finches will nest in cavities in *Eucalyptus* trees when they are available or make grass nests constructed in the canopy of these trees (Brazill-Boast *et al.* 2010). However, following on from a similar approach in the closely related zebra finch (*Taeniopygia guttata*) (Griffith *et al.* 2008), to facilitate the intensive study of the breeding ecology of this species and the Gouldian finch (*Erythrura gouldiae*) in this area we erected about 200 specially designed nestboxes (full details in Brazill-Boast *et al.* 2011).

Nesting

All nest boxes and known cavities in trees were checked for new nesting attempts every six days. Most of the recorded nesting attempts ($n = 377$; 88%) however were in nest boxes. Nests were monitored every 2-6 days (depending on the stage of the nest). Nests were checked daily from two days before the expected hatching date (12 days from the onset of incubation; Higgins *et al.* 2006). At the age of ten days all nestlings were banded, measured and weighed and a small blood sample was taken. All nests were checked just before fledging (age 16 days) and the nestlings present at that time were assumed to fledge.

Egg size (length and breadth) was measured for 40 eggs (measured in 2010 only) to the nearest 0.01 mm. The date the first egg was laid, clutch size, number of nestlings, number of un-hatched eggs, length of incubation and nestling periods, number of fledglings and date of fledging were recorded for all known breeding pairs. All nesting data were analyzed using the statistics program JMP. Inter nest distances were calculated with R Package (for multivariate and spatial analysis; Version 4.0), from points taken with a Garmin GPS unit (Garmin Gecko 301, Garmin Ltd., USA) in the field.

Site fidelity

Adult Long-tailed Finches were caught in mistnets along creeks and with handnets on their nests. All birds were banded with a metal band (supplied by the ABBBS) and a unique combination of three colour bands in order to later visually identify individual birds.

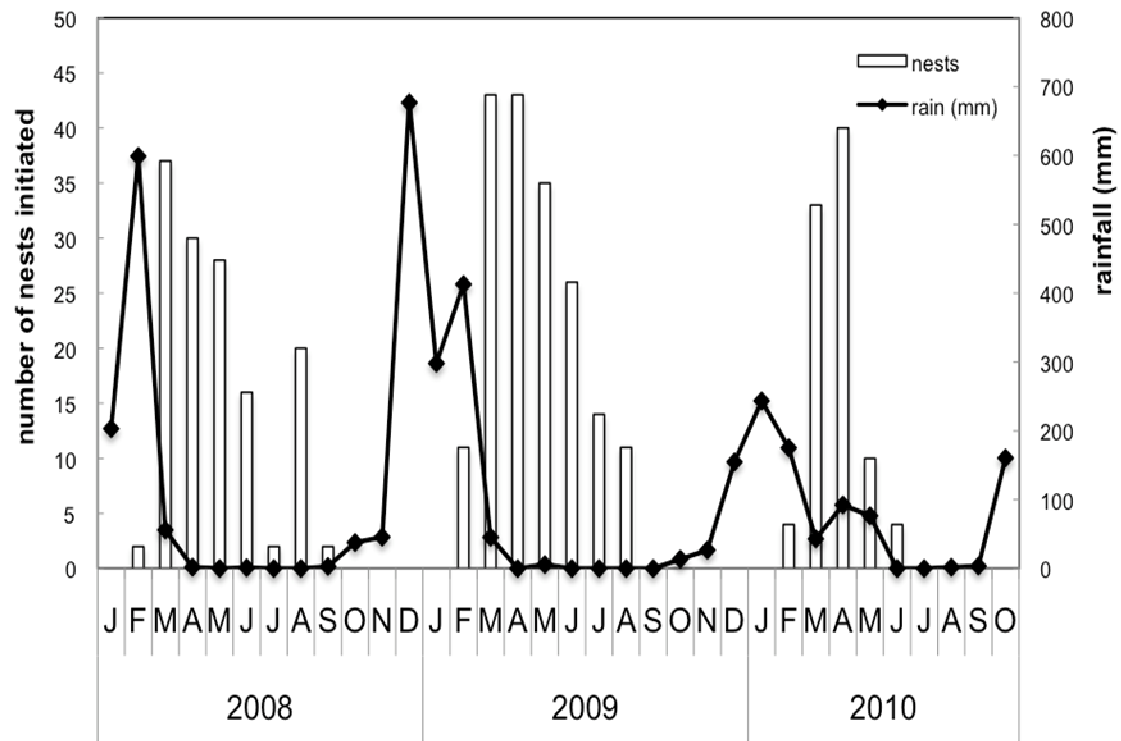


Figure 2.1a Initiations of new nests per months and rainfall per month.

First egg laying dates 2008-2010 and monthly rainfall (mm). Rainfall data from Bureau of Meteorology (www.bom.gov.au).

2.4 Results

Timing of breeding

Breeding was recorded from February till Sept (in 2008 and 2009) and from February till June in 2010. First recorded nesting attempts started (first egg) on 16 February (2008), 1 February (2009) and 3 February (2010), while last nesting attempts per season were recorded on 8 September (2008), 28 August (2009) and 19 June (2010). The peak of nest initiation (Figure 2.1a) was reached in March (in 2008), late March / early April (in 2009) and April (in 2010). The Kimberley has a tropical monsoon climate, usually receiving about 90% of its rainfall during the short wet season from November to March. The breeding season in 2008 and 2009 coincided with the dry season from March till October in those years. In 2010 there was an unusual pattern of rain likely connected with a strong La Nina event (Bureau of Meteorology), and breeding activity ceased in June in 2010 probably due to the very unseasonal rain in April, May and June of that year and/or the amount of rain in December/February.

Breeding success

During the three-year study period a total of 420 nesting attempts (136 in 2008, 190 in 2009, 94 in 2010) were recorded, with 377 in nestboxes (98 in 2008, 186 in 2009, 94 in 2010) and 40 in natural cavities (36 in 2008 and 4 in 2009). Of these nesting attempts 33.8% were successful ($n = 420$; 35% in 2008; 36.3% in 2009; 26.3% in 2010). Of the initiated nests in 2010 36 were the focus of manipulative experiments (to be reported elsewhere) and were therefore not included in the calculation of reproductive success.

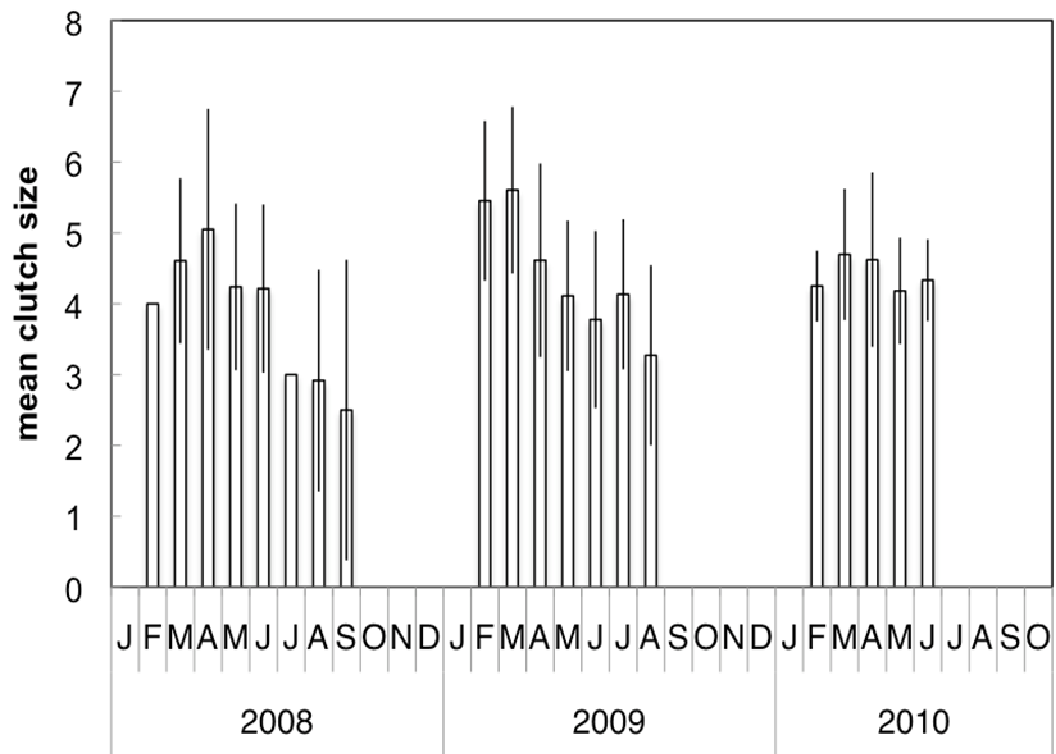


Figure 2.1b Mean clutch size per month (\pm se) for all three breeding seasons (2008 – 2010).

The cause of failure in the other nests was hard to determine, but either caused by parental desertion, predation of the nest or predation of (one of) the parents. Predation was assumed when the nest was found empty of eggs or nestlings before they were old enough to leave themselves. On only six occasions was predation directly observed, four times (twice in egg stage and twice with nestlings) by an olive python (*Liasis olivaceus*) and twice (both nestling stage) by a pied butcherbird (*Cracticus nigrogularis*).

The average length of a successful nesting attempt was 38.8 ± 3.5 days and it took on average 36 ± 15 days till re-nesting after a failed nest (min 17 days; $n=21$) and 79 ± 24 days after fledging of a successful nest (min. 45 days; $n=28$). In 2008 and 2009 nests were initiated over a period of 206 and 210 days respectively, but the total season was shorter in 2010 and only 137 days. Within a breeding season pairs could therefore potentially have up to three successful nesting attempts. We recorded pairs having between one and three nesting attempts per breeding season and in the more normal seasons (2008 and 2009) the percentages having multiple successful attempts were as follows: in 2008 26 pairs (81%) had one breeding attempt, six pairs (19%) two attempts and no pairs having three successful attempts; in 2009 34 pairs had one successful breeding attempt (76%), 8 pairs (18%) two attempts and three pairs (7%) three attempts. One pair had three nesting attempts in both 2008 and 2009 of which five were successful (two in 2008 and three in 2009), with this pair fledging a total of 13 offspring.

Clutch size, brood size and success per nest

Mean clutch size of successful nests was 4.66 ± 1.13 ($n = 132$, range 2 - 8) and clutches were on average smaller later in the season (Figure 2.1b; Table 2.1). Eggs were 11.2 ± 0.4 mm wide and 16.0 ± 0.6 mm long ($n = 40$). Hatching success (percentage of eggs hatched in nests

Table 2.1 Breeding success of Long-tailed Finches by clutch size in successful nest (fledged at least one offspring). ^a initiation day 1 is 1 March

	2	3	4	5	6	7	8	Stats	
								F _{6,131}	p
Number. of clutches	1	16	46	44	17	5	3		
Initiation day ^a	96	113 (47 – 177)	70 (-29 – 177)	50 (-17 – 132)	48 (-5 – 121)	51 (9 – 127)	13 (1 – 23)	5.37	< 0.001*
Number hatched (mean ± se)	2	2.6 ± 0.7	3.6 ± 0.6	4.4 ± 0.8	4.8 ± 0.9	5.8 ± 0.8	5.0 ± 1.0	24.02	< 0.001*
Number fledged (mean ± se)	2	2.6 ± 0.7	3.5 ± 0.6	4.3 ± 0.9	4.8 ± 0.9	5.8 ± 0.4	4.0 ± 1.0	20	< 0.001*
hatching success (%; mean ± se)	1	87 ± 24	90 ± 15	87 ± 18	80 ± 15	83 ± 12	83 ± 29	1.79	0.106
fledging success (mean ± se)	100	100	97 ± 9	97 ± 10	99 ± 5	100	83 ± 29	1.53	0.174
Incubation time (mean ± se)	11	13.9 ± 1.9	14.5 ± 2.7	13.0 ± 2.1	12.5 ± 1.2	14.0 ± 2.4	12	3.01	0.009*
Nestling time (mean ± se)	19	19.6 ± 1.4	20.5 ± 1.9	20.9 ± 2.4	20.1 ± 1.4	22.2 ± 1.3	22.0 ± 1.0	1.95	0.078
Length of breeding attempt (mean ± se)	32	37.0 ± 2.9	39.1 ± 3.4	39.2 ± 3.2	39.0 ± 2.2	43.2 ± 3.6	42.0 ± 1.0	3.96	0.001*

where at least one egg hatched) was $87 \pm 17\%$ and did not differ between years ($F_{2,64} = 0.773$, $p = 0.464$). In 47% of nests at least one egg hatched ($n = 200$).

Mean brood size was 3.98 ± 1.10 ($n = 132$, range 1 – 7), with an average of 3.87 ± 1.10 ($n = 132$, range 1 – 7) fledged offspring per successful nest. Mean clutch size ($F_{2,209} = 3.083$, $p = 0.049$), brood size ($F_{2,131} = 5.717$, $p = 0.004$) and number of fledglings per nest ($F_{2,131} = 5.040$, $p = 0.008$) did differ between years with lower means in 2008 than in 2009 and 2010.

Excluding the nests that failed completely, the fledging success (percentage of nestlings that fledged) was $98 \pm 9\%$ and did not differ between years ($F_{2,131} = 2.696$, $p = 0.071$), suggesting that there is negligible partial brood mortality in this species. Overall, however only 31.8% of nests in which eggs were laid fledged any young ($n = 420$). Clutch size affected the number of eggs hatched and number of offspring fledged, with success peaking around a clutch size of seven (Table 2.1). Incubation time differed between clutch sizes and nestling time tended to differ, therefore the total length of the breeding attempt differed as well (Table 2.1). Annual breeding success was between 26.8 – 40.8% of eggs laid resulting in fledged offspring – an overall average of 33.6% of all of the eggs laid resulting in fledged young across these three breeding seasons.

Success of nesting attempts did differ between attempts in natural cavities and nest boxes with attempts in natural cavities more likely to fail completely ($\chi^2 = 29.40$, $df=1$, $p=0.005$; only 2008; cavity $n=36$; box $n=99$). Nests in natural cavities and nest boxes did not differ in clutch size ($F_{1,102}=0.0$, $p=0.99$), brood size ($F_{1,100}=0.27$, $p=0.61$) or number of offspring fledged ($F_{1,100}=0.40$, $p=0.53$). Nor did they differ in hatching success ($F_{1,61}=1.55$, $p=0.22$); fledging success in those nests that survived to that stage ($F_{1,61}=0.37$, $p=0.55$); or the duration of the nesting attempt.

Table 2.2 Number of banded breeding pairs and banded nestlings per breeding season and number of returning banded adults and nestlings of the previous year.

	banded pairs breeding	pairs from previous year breeding	nestlings banded	nestlings from previous year breeding (% of banded nestlings)
2008	42		130	
2009	65	25 (60% from 2008)	307	5 (3.8%)
2010	54	19 (29%) + 11 (26% from 2008)	58	11 (3.6% of 2009) + 2 (1.5% of 2008)

Although birds matured very quickly (near complete adult plumage within three months; pers. obs.) none of the individuals banded as a nestling were found breeding in the same breeding season in which they hatched. In 2008 and 2009 the earliest hatched young would have been about 190 days old while some adults were initiating the last clutches of the year. In the year after they hatched 16 individuals (9 Female; 7 Male) were found breeding in the study site. The youngest female found breeding was 264 days old (nearly nine months) and the youngest male 332 days old (just over 11 months). For those individuals for which we knew a hatch date the average age at first breeding was 330 ± 37 days old (mean Female 316 days old and mean Male 348 days old).

Site and mate fidelity

Colour banding of Long-tailed Finches in our study area started early in the 2008 breeding season and continued throughout the 2009 and 2010 breeding seasons (Table 2.2). Mate fidelity was high with 39 pairs (of 106 banded pairs; 37%) breeding together multiple times within a season and 55 pairs (52%) breeding together in multiple years, with one pair observed to breed together three years in a row. Birds were observed breeding with a different partner in several cases (17 Females; 8 Males), but none of the former partners were seen again and were presumed dead.

Site fidelity was also high with 60% and 29% of banded pairs respectively breeding in either 2008 and 2009 breeding remaining to breed in the area in the subsequent year. In addition, 26% of pairs breeding in 2008 were also still present and breeding in the area in 2010 (Table 2.2). Of the nestlings banded in 2008 and 2009 3.8% and 3.6% respectively were found breeding in the same sites the next year, with 1.5% still breeding there two years later (Table 2.2).

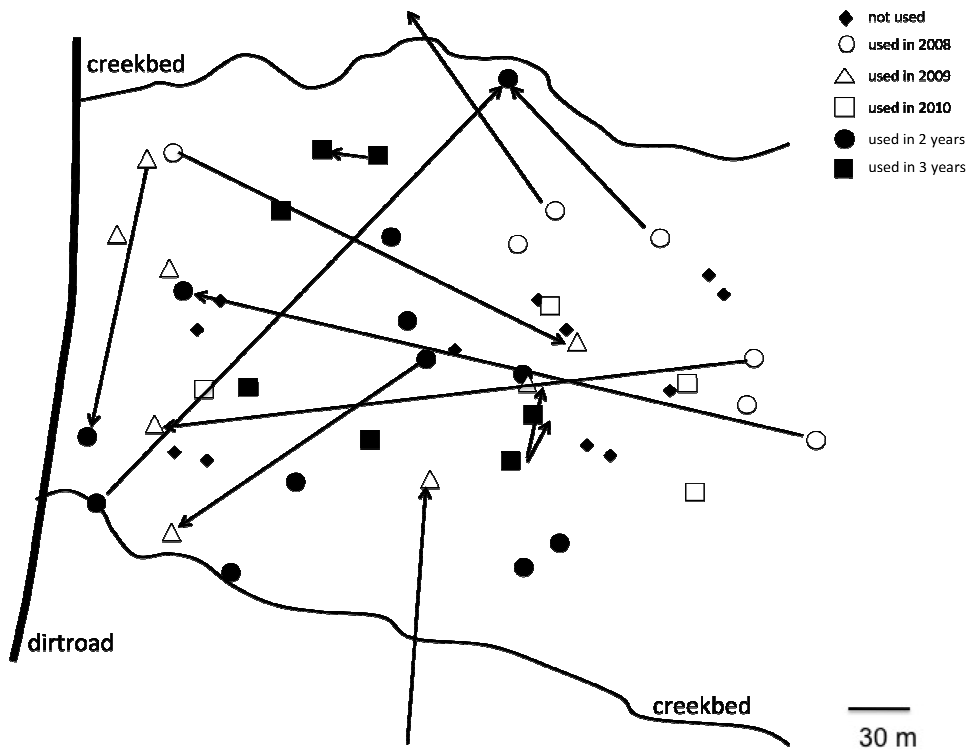


Figure 2.2 Map of nest box distribution and use of nest boxes over part of the field site from 2008 - 2010.

Intensity of use of nest boxes indicated by markers (diamond: not used; open circle: only used in 2008; open triangle: only used in 2009; open square: only used in 2010; filled circle: used in two years; filled square: used in three years). Movement of banded pairs between nest boxes between breeding seasons indicated by arrows.

Site fidelity for the same nest box was also high with one 2009 nestling (a female) nesting in 2010 in the same box she hatched in the previous breeding season. Eight pairs nested in the same box more than once within a season (5 after a successful attempt; 3 after a failed attempt); and seven pairs nested in the same box between seasons. One pair nested three times in the same box (twice successful; in 2008 and 2009). When re-nesting with different partner: two males nested in the same box between seasons; two females nested in the same box (one within and one between seasons). When re-nesting in a different nest site: movement between nest sites within years was on average just 265m ($n=58$; range 0-1708m); between years on average 235m ($n=34$; range 0-951) (Figure 2.2). Some nest boxes were used more often than others, with 22 (of 200; 11%) being used in all three breeding seasons, 37 (19%) used in two breeding seasons, 60 (30%) used in only one breeding season and 81 (41%) never used (Figure 2.2). Breeding densities were relatively low ranging from 0.03 (end of season) to 0.4 nests ha^{-1} (at the peak of the season) over the whole study site (108 ha) with usually just one nest per tree (nest box density was 1.9 ha^{-1}). On only one occasion were two active nests found in the same tree (one a freestanding grass nest in the canopy and one in a nestbox).

2.5 Discussion

The Long-tailed Finch population studied in the Eastern Kimberley were found to breed seasonally from February till September in most years, which is similar to the two populations previously studied in the Northern Territory (Tidemann & Woinarski 1994). This is most likely linked to food availability, as the abundance of food (seeds and insects) in the monsoonal tropics is extremely seasonal (Woinarski & Tidemann 1992), with seed availability reaching a peak at the end of the wet season (February) and becoming scarce at the end of the dry season (around October) (Tidemann & Woinarski 1994). In 2010 the breeding season was shorter (ending in June) likely due to the exceptional unseasonal rain

during the dry season, which probably affected food availability by e.g. washing away the seeds. This pattern of highly seasonal breeding contrasts nicely with the closely related and well-studied Zebra Finch, *Taeniopygia guttata*, that fills a similar ecological niche to the Long-tailed Finch, in the more arid areas of Australia. Reproduction in that species also reportedly responds to the availability of ripening grass seeds (Zann *et al.* 1995), although in more predictable areas of the arid zone they are also found to show quite a high level of seasonality in reproductive timing (Zann 1996; Griffith *et al.* 2008).

Following on from a similar approach in the closely related Zebra Finch (Griffith *et al.* 2008), to facilitate the intensive study of the breeding ecology of this species and the Gouldian Finch in this area we erected about 200 specially designed nestboxes (full details in Brazill-Boast *et al.* 2011). As with the Zebra Finch, the Long-tailed Finch readily accepted the nest boxes, and indeed preferred them to natural sites with only four breeding attempts recorded in natural cavities the year after the nest boxes were erected, versus 189 initiated in nest boxes. We are aware that the provision of nest boxes can create several biological artefacts resulting from, for example, unnatural breeding densities, nest-parasite dynamics, and reduced predation (Møller 1989). Density of nesting sites was only slightly increased in the study area by the provision of nest boxes, but this species does not only nest in natural cavities but also nests in grass nests in the foliage of trees (Immelmann 1965; Brazill-Boast *et al.* 2010), resulting in a virtually unlimited number of available nesting sites. We did find that nesting attempts in natural cavities were more likely to fail than nesting attempts in artificial nest boxes, which was also found for Zebra Finches breeding in nest boxes compared to free standing nests (Griffith *et al.* 2008), and in both cases was presumably due to the reduced vulnerability of nests in boxes to predation. We did not find increased clutch size and fledging success for the nesting attempts in nest boxes, however the sample size was small for attempts in natural cavities. Clutch size was larger when breeding in boxes for Zebra Finches but this was

recorded for different years and might have reflected differing conditions between years (Griffith *et al.* 2008).

The breeding densities of Long-tailed Finches were relatively low and the breeding pairs seemed to space themselves out evenly across the available boxes. Even at the time of peak reproductive effort over 40% of boxes were unoccupied and therefore pairs could have found a vacant box nearer to an active pair had they wished to nest at a higher density. At the time of peak activity the density of breeding pairs was only about 0.4 nests ha⁻¹, which is much lower than studied populations of the zebra finch in which multiple nests are frequently found within a single tree and breeding densities frequently exceed 20 nests ha⁻¹ (Zann 1994; Griffith *et al.* 2008).

Overall, we found that only about 33% of initiated nesting attempts were successful in producing any fledglings, suggesting a high rate of predation and/or a high propensity for desertion of an individual reproductive attempt. When pairs were successful in rearing offspring, they virtually always succeeded in raising all of their nestlings. This pattern of reproductive success is very similar to those described in the Zebra Finch, both in natural nests and nest boxes (Zann 1994; Griffith *et al.* 2008). The use of nest boxes in this study did not reduce the risk of predation by snakes, but likely reduced the predation by birds as the entrance to the boxes were usually longer than many of the natural cavities used by this species, which can be shallow and quite fragile (Brazill-Boast *et al.* 2010). The only other species that used the nest boxes erected in this study was the Gouldian Finch, which shared the same area and natural nesting cavities (Brazill-Boast *et al.* 2010) and is the subordinate competitor for access to nest hollows. Therefore we do not believe that the presence of the Gouldian Finch in this area particularly affected the breeding density of Long-tailed Finches.

We recorded pairs having between one and three nesting attempts per breeding season. The clutch size was very similar to those reported for Zebra Finches (Zann 1994, 1996; Griffith *et al.* 2008), and as in that species, and many other birds, also declined in size later in the season, presumably as a consequence of a reducing food availability (Lack 1966). In successful nests, both hatching success (87% of eggs hatched) and survival of hatchings (>98%) were very high, and again mirrored the pattern observed recently in the Zebra Finch (Griffith *et al.* 2008). In contrast to studies of the Zebra Finch, which are unable to track individuals over an extended time because of their high mobility, we were able in this study to estimate the overall annual breeding success of the individuals in a population and find that one third of all eggs laid in a year resulted in fledged young. It will however require a bit more effort over a longer period to derive a good estimate of how many of these young survive to maturity and become reproductively active themselves.

Although Long-tailed Finches matured quickly, reaching near adult plumage within three months of hatching, none of the individuals banded as nestlings were found breeding in the same breeding season they hatched, even though some young would have been about 190 days old towards the end of the breeding season. In the Zebra Finch, in a prolonged breeding event in one location, young Zebra Finches of about 70 days old were reported to breed (Zann 1994). The youngest female Long-tailed Finch that we found breeding was nearly nine months old. This different strategy in these two species might be related to the difference in the mobility of the species and the predictability of their breeding season. As breeding is more opportunistic for Zebra Finches it pays off to mature quickly and have a breeding attempt as soon as possible. Long-tailed Finches however have a more predictable and longer breeding season starting at the same time each year. Therefore, the chance of young birds breeding late in the season being successful is low, and their attempt might jeopardise their chance of survival to the following breeding season.

We found a high level of philopatry in this species, with 60% of pairs breeding in the same area the next season, and often within the same box. Both males and females nested in a box previously used when re-nesting with a new partner, therefore both males and females seem to have a role in nest site selection. It is unknown whether Long-tailed Finches stay in the same area during the remainder of the dry season, and throughout the wet season. Recruitment of banded nestlings to the local population was lower than the site fidelity of adults but again some individuals remained within an area of a few hundred metres of where they hatched.

Mate fidelity was high with pairs observed breeding together multiple times per season and over multiple breeding seasons. In some cases an individual was seen with a new partner, while the former mate was not seen again. Given the high level of site fidelity observed in adults, it is reasonable to assume that the missing partners may have died and that these cases do not represent divorce. The pair bond in this species appears to be very strong and pairs were typically observed acting as a single unit with partners following each other and performing all activities simultaneously including foraging and preening, as previously described by Immelman (1965) and Zann (1977) for both Long-tailed Finches and Zebra Finches. Familiarity with a long time partner might affect the success of the breeding attempts through better synchronisation of the partners. In the Zebra Finch, the pair bond appears to be similarly strong and maintained by complex vocalisations between the pair (Elie *et al.* 2010), and results in a low level of extra pair paternity (Griffith *et al.* 2010).

Through our intensive field research of a breeding population of the Long-tailed Finch, we have been able to describe for the first time some of the important reproductive parameters of one of the more common estrildid finches occurring in the tropical northern savannah of Australia. This basic data is important to further our understanding of Australian biodiversity. Even for a family as well recognised as the estrildid finches there have been surprisingly few

studies of most species. For example, even a widespread species like the Diamond Firetail *Stagonopleura guttata*, in the more populated southeast of Australia has only recently been the focus of intensive behavioural studies (e.g. Cooney & Watson 2005; McGuire & Kleindorfer 2007; Stirnemann *et al.* 2009). The Long-tailed Finch is the focus of previous and current studies of signalling and sexual selection (e.g. Langmore & Bennett 1999; Van Rooij & Griffith 2010) and in addition makes an interesting and important contrast with the closely related, but ecologically different Zebra Finch, which has now become one of the most important avian model systems in the world (Griffith & Buchanan 2010). Finally, the Long-tailed Finch is sympatric with the remaining populations of the endangered Gouldian Finch and recently recognised as a potential threat to that obligate cavity nester, as a dominant competitor over access to the increasingly scarce resource of good quality nest hollows (Brazill-Boast *et al.* 2011).

2.6 Acknowledgements

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CHAPTER THREE

First record of cooperative breeding in an Australian Estrildid



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3.1 Abstract

Long-tailed Finches (*Poephila acuticauda*) breeding in natural cavities and nest-boxes were monitored during the breeding season, between March and September 2008, as part of an ongoing field study near Wyndham, northern Western Australia. Towards the end of the breeding season, two adults and their son, who had fledged 4 months earlier, were observed together over many days feeding nestlings (10–17 days old) produced by the adults in another breeding attempt. This is the first description of cooperative breeding in an Australian estrildid finch. Based on these observations, we do not intend to suggest that the Long-tailed Finch should be considered a cooperatively breeding species, but such data help us to understand the variation that exists with respect to familial relations and parental care and provides a foundation for work addressed at understanding the evolutionary origins of cooperative behaviour in birds.

3.2 Introduction

Cooperative breeding is particularly common in Australian birds, occurring in ~93 species, or some 12% of the total species recorded in Australia (from data in Cockburn 2006) as opposed to 9% worldwide (Cockburn 2006). In a recent and fairly comprehensive review of the breeding system of the oscine passerines (Cockburn 2003), all Estrildinae (Passeriformes: Estrildidae) were considered exclusively pair breeding, with only some rare cases of helping behaviour recorded in two congeneric African estrildids (Grey-headed Nigrita (*Nigrita canicapillus*) and Chestnut-breasted Nigrita (*N. bicolor*)) and a few instances where multiple females laid in the same nest (e.g. Swee Waxbill (*Estrilda melanotis*)) (Fry & Keith 2004).

To date, no form of helping behaviour has ever been recorded for any of the 18 species of native Australian estrildid finch (Russell 1989; Arnold & Owens 1998; Cockburn 2003, 2006), with no previous study finding more than two individuals feeding offspring at a single nest (A. Cockburn, pers. comm., 13 October 2008). This is consistent with the suggestion (Cockburn 2003) that estrildine species are among the least likely to breed cooperatively, as they belong to a group that crossed to Australia over Wallace's Line (the biogeographical boundary that separates the zoogeographical regions of Asia and Australia). Estrildines are therefore likely to be derived from highly mobile colonist species that by their nature are likely to be pair breeders, as opposed to true cooperatively breeding species that tend to be permanent residents (Clarke 1997). In addition, cooperative breeding is most likely to occur in long-lived (Arnold & Owens 1998) and sedentary species in which individuals are likely to live in close proximity with kin. Despite this, however, we here describe the first observations of three individuals feeding nestlings at a nest in an Australian estrildid, the Long-tailed Finch (*Poephila acuticauda*).

3.3 Methods

Long-tailed Finches nesting in natural hollows and nest-boxes (put up to facilitate this study) were observed during the breeding season, which extends from early March till the end of September, in 2008 in the East Kimberley, near Wyndham, northern Western Australia (15°33'0" S, 128°08'0" E). Long-tailed Finches normally breed in pairs and are thought to have a very strong, socially monogamous pair-bond, potentially mating for life (Zann 1977). Near the end of the breeding season (September), three individuals were observed feeding young at a nest-box containing four nestlings that hatched on 8 September.

The two adults visiting the nest had been marked with an individually distinct combination of colour-bands (and a metal band supplied by the Australian Bird and Bat Banding Schemes (ABBBS), Canberra) during a previous successful breeding attempt at a different nest site (64 m away). This pair had fledged two offspring (one male, one female) on 24 May. The third individual visiting the nest was only banded with a single metal band (in our study all nestlings were only banded with a metal band). On 23 September, the 'extra' bird was caught and colour-banded while visiting the nest, and from the ABBBS band-number was identified as the 4.5-month-old male offspring from the earlier recorded nesting attempt (hatched 3 May). Although this individual had, by September, moulted into its adult plumage and attained adult bill colouration, for clarity we will hereafter refer to it as the juvenile male. As Long-tailed Finches are sexually monomorphic (Langmore & Bennett 1999) all individuals were sexed using the molecular sex markers p2 and p8, using well-established techniques (Griffiths *et al.* 1998).

Table 3.1. Summary of observations of feeding of nestlings by parents and juvenile male during 23.5 hours of observation over 6 days (18–25 September 2008)

Feeding bouts were the time from entering the nest to feed the young until leaving the nest after feeding. Figures are means + s.e.; n.s., not significant

	Number of feeding bouts	Mean number of feeding bouts per day	Average duration of feeding bouts (min)	Average interval between feeding bouts /h (number of intervals observed)
Juvenile male	8	4.1	2.81 ± 0.62	1.57 ± 0.07 (n = 3)
Adult male	7	3.6	1.86 ± 0.73	3.45 ± 0.25 (n = 2)
Adult female	7	3.6	2.10 ± 0.63	1.60 ± 0.010 (n = 2)
Significance		n.s.	n.s.	Juvenile v. female: n.s. Juvenile v. male: $P < 0.01$

Direct observations of the nest were made on three days (18, 21 and 23 September 2008) starting when the nestlings were 10 days old, at a distance of 15 m from the nest using 10 x 40 binoculars, over a total of 11 h, ranging from 2.5 to 3.5 h day⁻¹. The number of behavioural observations is limited by the low rate at which Long-tailed Finches feed their nestlings (<1 visit to the nest per hour (E. P. van Rooij, pers. obs.)). On three other days (22, 24 and 25 September 2008) the nest was filmed with a video-camera erected in the tree within a few metres of and directed at the entrance to the nest. Recordings were made for between 3.5 and 4.5 h per day, for a total of 12.5 h. Differences between individuals in the number and duration of feeding bouts per day were analysed using two-way analysis of variance (ANOVA). The length of intervals between feeding bouts were compared between individuals using t-tests. All means are presented \pm s.e.

3.4 Results

On five of the six observation days, all three individuals were observed feeding the nestlings. On the remaining day no birds were observed feeding the nestlings. During the 23.5 hours of observation, the nestlings were fed a total of 22 times by the three birds (Table 3.1). All three individuals visited the nest together 10 times over the period of observation, and the young were fed by at least one individual each time. The juvenile male fed the young on eight occasions, always after one of the parents had just fed the young. The parents fed the young seven times each. On four occasions all three individuals fed the young, on four occasions one of the parents and the juvenile fed the young and on the other two occasions only one of the parents fed the young.

The mean number of feeding bouts per day for all three birds combined was 3.7 ± 0.2 (s.e.; $n = 22$ individual bouts over 6 days), with an average length of 2.29 ± 0.37 min. The nestlings

were heard begging during all observations of feeding. There was no significant difference between the juvenile male or adults in the duration of feeding bout ($F(2,13) = 0.56$, $P > 0.50$; Table 3.1). The mean interval between feeding bouts of the juvenile male did not differ significantly from that of its mother ($t = 0.29$, $P > 0.5$), but the mean interval was shorter than that of its father ($t = -9.18$, $P < 0.01$) (Table 3.1). The juvenile male was often observed sitting close to one or both of the adults and was involved in allopreening sessions, indicating it was readily accepted by the adults.

3.5 Discussion

These observations describe a single case of helping at the nest by a juvenile male from a previous nest in the Long-tailed Finch. The results show that the juvenile male invested at least as much in this brood as each of the adults in terms of feeding. Similar situations with juveniles feeding their parents' later offspring have been found in Dusky Moorhens (*Gallinula tenebrosa*) (Putland & Goldizen 2001) and Buff-breasted Wren (*Thryothorus leucotis*) (Gill 2004). To date, the observations reported here are the only occasion where more than two individuals were recorded supplying food to nestlings in this traditionally pair-breeding species (out of 50 nests where we observed feeding bouts over several days).

We do not believe that a shortage of territories or mates (habitat saturation) caused this occurrence of cooperative breeding, as would be predicted by the ecological-constraints hypothesis (Emlen 1982). Little is known about the movements of this species, but they have been described as largely sedentary with little dispersal (Higgins *et al.* 2006). There were enough suitable available nesting sites present in the breeding area (180 cavities and 200 nest-boxes; E. P. van Rooij, unpubl. data), and it seems unlikely that the availability of potential mates might have been the limiting factor, with large numbers of juveniles being produced in

this area and moving around to drink at increasingly scarce waterholes at the end of the dry season.

This juvenile male, although independent, probably remained near its parents for a prolonged period until its parents' next breeding attempt, which is one way for cooperative breeding to arise (Cockburn 1998). Typically, in Long-tailed Finches, offspring were observed to stay with their parents for several weeks after fledging (E. P. van Rooij, pers. obs.). However, the nest described above was the only one of eight nests observed in the same period where more than two individuals were observed around the nest and helped feed the new nestlings. Four other pairs were known to have a second successful breeding attempt, where we also recorded parental care, but in none of these was a juvenile or juveniles fledged in an earlier brood seen with the parents or near the nest of a later attempt.

We do not think it likely that the use of nest-boxes increased the proportion of second clutches and affected the occurrence of helping behaviour in this species. Density of nesting sites was only slightly increased in the study area by the added nest-boxes, but this species does not only nest in natural cavities but also nests in grass nests in the foliage of trees (Immelmann 1965), resulting in a virtually unlimited number of available nesting sites. Besides this, only a very small proportion (2.1%) of the available natural cavities and nest-boxes were occupied when the helping behaviour was recorded. Without the availability of extra available nest sites (in the form of nest-boxes) there would still be enough opportunity to have second clutches. We, therefore, do not think it likely that the use of nest-boxes increased the proportion of second clutches and affected the occurrence of helping behaviour in this species.

The most important factor in this occurrence of helping at the nest is probably the timing of the breeding attempt. The breeding season was coming to an end, most likely as the availability of food and water was reduced and these observations were made at one of the last two nests from which young fledged during the breeding season of 2008. The juvenile male would therefore be running out of time to start its own breeding attempt and could potentially gain more from helping its parents raise a new brood of siblings.

At this stage we certainly do not intend to suggest that the Long-tailed Finch should be considered a cooperatively breeding species based on this single observation. However, observations such as these help us to understand the variation that exists in nature with respect to familial relations and parental care and helps to provide a foundation for work addressed at understanding the evolutionary origins of cooperative behaviour in birds.

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CHAPTER FOUR

Are Long-tailed Finches really monomorphic?



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4.1 Abstract

Studies of sexual selection have focused mainly on dimorphic and / or polygynous species, where males, typically possess more exaggerated secondary sexual characters. However in many species, receiving far less attention, the expression of ornamental traits by females matches that in males. Several hypotheses have been proposed to explain sexual monomorphism, including mutual mate choice, genetic correlation, weak sexual selection and sexual indistinguishability. The sexual indistinguishability hypothesis suggests that sexual monomorphism is an adaption to avoid competition in monogamous flock-living species. Based on measurements of museum skins and domesticated birds in Europe, the Australian long-tailed finch was classified as a sexually monomorphic species, providing the best empirical support for the sexual indistinguishability hypothesis. Using both domestic and wild long-tailed finches, we have re-evaluated the extent to which the sexes are really indistinguishable. Morphological measurements of wing, tail, tail streamers, tarsus, bill and patch size, and colour spectrometric measurements of the yellow upper mandible and grey crown, were compared between the sexes. While the sexes are similar, males and females nonetheless differed in seven of ten traits in wild populations. In domestic populations, the sexes differed to a lesser extent but were still significantly different at three of ten traits, and discriminant analysis showed that 92% of wild individuals and 89% of domestic individuals could reliably be sexed based on just these morphological traits. Contrary to previous work, this study demonstrates that wild long-tailed finches are sexually dimorphic, and that the similarity between males and females in this species cannot be explained by the sexual indistinguishability hypothesis.

4.2 Introduction

In over half of the world's bird species, females appear identical to males and consequently do not show clear differences in sex-linked morphology (Griffiths *et al.* 1998). More recently, however, through the use of techniques that permit more detailed quantitative analysis of morphological variation, subtle differences between the male and female in many of these apparently monomorphic species have been found (Madden *et al.* 2004). The other extreme, sexual dimorphism, is where there are clear differences in form, size or colour (Hunt *et al.* 1998) between individuals of different sex in the same species. The causes of these differences have intrigued researchers since Darwin's (1871) extensive review of the remarkable variation across species with respect to monomorphism and (the presence and extent of) sexual dimorphism. Sexual selection studies have focused mainly on dimorphic and /or polygynous species, where selection is expected to work only on males, who therefore possess the more exaggerated secondary sexual characters. Monomorphic species, where females express ornamental traits to a similar extent as males, have received far less attention (Clutton-Brock 2007, 2009; Kraaijeveld *et al.* 2007). However, it seems likely that the mechanisms responsible for the evolution of secondary sexual characters in females are similar to those operating in males and include intra-sexual competition between females for breeding opportunities and competition to attract mates (Clutton-Brock 2009).

Several hypotheses have been developed to explain the existence of monomorphism and mutual ornamentation. The genetic correlation hypothesis suggests that elaborate monomorphic characters are functional in only males (e.g. in mate choice or status signalling), while the corresponding female characters are non-functional and expressed only because of shared genetic architecture (Lande 1980; Lande & Arnold 1985). Evidence for a genetic correlation in the expression of ornamental traits has been found in some species

(Cuervo *et al.* 1996; Roulin *et al.* 2001) but not others (Tella *et al.* 1997).

Another possible explanation for monomorphism, particularly in species where the sex roles are similar and adults do not differ markedly from juveniles in appearance, is that sexual selection is weak relative to natural selection counteracting the evolution of highly prominent or costly ornamental traits (Andersson 1994).

A third possibility is that the existence of ornamental traits expressed in both sexes may be favoured by mutual sexual selection driven by both female and male competition for mates (Darwin 1871; Trail 1990). Mutual mate choice has been confirmed in several monogamous, sexually monomorphic species e.g. crested auklet *Aethia cristatella* (Jones & Hunter 1993), bearded tit *Panurus biarmicus* (Romero-Pujante *et al.* 2002) and black swan *Cygnus atratus* (Kraaijeveld *et al.* 2004). Male choice for more colourful females was demonstrated in the slightly dichromatic bluethroat *Luscinia s. svecica* (Amundsen *et al.* 1997), and in the monomorphic king penguin *Aptenodytes patagonicus* mate choice was stronger in females (Pincemy *et al.* 2009).

Although each of the above ideas are likely to play a role in the evolution or maintenance of sexual monomorphism, Burley (1981) explained the absence of morphological sex markers with the sexual indistinguishability hypothesis, suggesting that sexual monomorphism is an adaptation to avoid competition in flock-living and/or colony-breeding species. Individuals might benefit by being able to conceal their sex, as repeated interactions because of sexual competition would sometimes be disadvantageous (Burley 1981), arguing that the advantages of indistinguishability depend on group size and the type of mating system and are expected to be greatest in monogamous group-living species (Burley 1981). Björklund (1984) criticized many of the assumptions behind this hypothesis, and the way in which Burley (1981)

suggested should be tested, concluding that identical selection pressures in the two sexes might not be necessary, and the absence of sex-dependent strong selection pressures might be enough (and reasonable in a monogamous species). Moreover, slight differences in selection pressures may only produce small differences in appearance, such that the species may appear monomorphic, at least to humans (Björklund 1984). Besides this criticism, several studies have rejected the theory after discovering slight sexual dimorphism in species with mutual ornamentation (e.g. red-tailed tropicbird *Phaethon rubricauda* Boland *et al.* 2004). Furthermore, the finding of clear sex recognition in several monomorphic species including feral pigeons (Nakamura *et al.* 2006) has further questioned whether seemingly monomorphic species are indeed indistinguishable. Although a number of studies have reported support for the idea of Burley's (1981) hypothesis, none of these have provided unequivocal empirical evidence. For example, in a study on mate choice in St. Peter's fish *Sarotherodon galilaeus*, concealment of sex was suggested as an explanation for the formation of homosexual pair bonds, but no behavioural evidence was provided (Ros *et al.* 2003). The only rigorous support that sexually monomorphic group-living species are unable to distinguish sex comes from Burley's (1981) study of feral pigeons and a later study of the long-tailed finch (Langmore & Bennett 1999).

The long-tailed finch is an Australian estrildid finch, which is generally described as monomorphic with respect to size and the coloration of plumage and bill (Immelmann 1965). Langmore & Bennett (1999) were the first to experimentally test the sexual indistinguishability hypothesis using domesticated long-tailed finches in the United Kingdom. In their study, Langmore & Bennett (1999) were not able to reliably distinguish between males and females on the basis of morphology, or by analysis of reflectance spectra from the grey head plumage and yellow bill. Langmore & Bennett (1999) also experimentally tested whether males concealed their sex by introducing a familiar or unfamiliar male or an

unfamiliar female to either a group of males or a single male, while scoring the number of courtship displays and the response of the recipient of the courtship. Males courted and copulated with unfamiliar males and females more than the familiar male, while newcomer males, especially subordinates, were more likely to reveal their sex to a single unfamiliar male and conceal their sex when entering a group (Langmore & Bennett 1999). Based on these experiments, they suggested that males are unable to distinguish sex without behavioural cues, and therefore conceal their sex to reduce harassment (in a group) and male-male conflict (when faced with another male) (Langmore & Bennett 1999). However, the classification by Langmore & Bennett (1999) of the long-tailed finch as sexually monochromatic, and the consequent support that this provides for the sexual indistinguishability hypothesis, has been criticized. Santos & Lumeij (2007) evaluated the extent of sexual monomorphism in the long-tailed finch and they found the grey crown to be significantly dimorphic for two of three tested angles and indicated sex correctly for between 72% and 76% of individuals. A further confounding problem with the studies of both Langmore & Bennett (1999) and Santos & Lumeij (2007) is that the focal individuals used were from domestic stock bred by amateur finch breeders in the United Kingdom and Netherlands, respectively. There is a possibility that these individuals might no longer show the natural occurring variation in morphological traits and therefore not represent the appropriate evolutionary background in which the traits evolved.

The controversy over the level of sexual dimorphism in the long-tailed finch (Santos & Lumeij 2007) is important because to date this species provides the only support (Langmore & Bennett 1999) for the sexual indistinguishability hypothesis (Burley 1981) with the exception of Burley's own work on pigeons (Burley 1981) which have since been shown to reliably be sexually dimorphic (Nakamura *et al.* 2006). To determine whether this species is truly monomorphic with respect to morphology, as well as plumage and bill reflectance, we

assessed variation between individuals from a population of wild long-tailed finches. To assess the possible effect of domestication on the level of sexual monomorphism, we also measured individuals from a domestic population acquired from Australian finch breeders. We compared morphological and spectrophotometric measurements between males and females that had been molecularly sexed for each population. We tested whether (1) domestic and wild long-tailed finches are sexually monomorphic, and (2) if not, on the basis of which traits males and females can be reliably distinguished?

4.3 Methods

Species and Study Area

The long-tailed finch is a common estrildid finch endemic to Northern Australia (Immelmann 1965; Higgins *et al.* 2006). They are socially monogamous with a very strong pair bond (Zann 1977), with pairs accompanying each other during the breeding season and within flocks during the non-breeding season.

Long-tailed finches were studied during the breeding season between early March and the end of September 2008 in the Eastern Kimberley, near Wyndham, Western Australia (S15°33'38", E128°08'59"). During the breeding season, nesting individuals were caught either on their nest with handnets or near their nest with mistnets (when nestlings were at least 10 d old), or during the dry season, with mistnets at waterholes. We sampled 208 wild adult individuals (81 females, 127 males) during the breeding season. We also measured 44 domesticated birds (21 females, 23 males) that had been sourced from Australian finch breeders.

Molecular Sexing

A blood sample (<20 µl) was taken from the brachial vein (wing) of adult birds and used to reliably determine their sex with the molecular sex markers P2 and P8, a well-established technique (Griffiths *et al.* 1998). As in other species, female samples resulted in the amplification of two products (size 355 and 400 bp) and males in only one (size 355 bp). The reliability of the sexing was confirmed by the observation that in each case in which two adults were caught on an active nest one was a female and one was a male (n = 40).

Morphological Measurements

The degree of sexual monomorphism was assessed across a number of morphological traits. Wing length was measured from the carpal joint to the tip of the longest primary (0.1 mm). Tail length was measured from the base of the tail to the tip of the longest rectrix (0.1 mm). Streamer length was measured from the length of both elongated pintail feathers (0.1 mm). Tarsal length was measured from the middle of the mid-tarsal joint to the distal end of the tarso-metatarsus (0.01 mm). Bill length was measured from the tip of the upper mandible to the anterior edge of the cere (0.01 mm). Bill depth was taken from the bottom of the lower mandible to the top of the upper mandible (0.01 mm). All birds were weighed (0.01 g) with either a pesola balance or a digital scale.

Patch size was measured from photographs taken with a Panasonic Lumix TZ3 digital camera (7 mega- pixel). Photographs were taken of each individual in the same posture, restrained in an artificial holder with the head tilted back. The number of pixels of the patch was then measured using the freehand selections tool and area measure option in the pro- gram ImageJ (version 1.40G). As the distance at which the picture was taken (approx. 20 cm) was not



Figure 4.1 Long-tailed Finch (*Poephila acuticauda*) male (right) and female (left).

constant, a ruler was attached to the bird holder. The number of pixels constituting 1 cm was calculated using the straight-line selections tool in ImageJ. The area of the badge (mm^2) was then calculated. To test the validity of this method, we photographed 20 domestic birds while sitting in a natural posture on a perch in a small cage. Patch size (in number of pixels) was then calculated from pictures using the freehand selections tool and area measure option in the program ImageJ. The results obtained with this method were highly correlated to those obtained when measuring the constrained bird in the holder (Pearson correlation: $r = 0.76$, $N = 20$, $p < 0.0001$).

Spectrophotometric Measurements

Owing to the difference between avian and human vision (e.g. UV reflectance may contain 'hidden' plumage sexual dichromatism; (Andersson *et al.* 1998; Cuthill *et al.* 1999), we used an optical spectrometer to assess reflectance objectively, including the UV spectrum. Plumage reflectance was measured from live birds. Two regions were measured, the yellow upper mandible and the grey crown. Yellow upper mandible reflectance was measured three times per individual on the same spot on the upper mandible and grey crown reflectance was measured three times on the same spot on the top of the head. A total of 75 males and 56 females were measured. A USB2000+ Miniature Fiber Optic spectrophotometer (Ocean Optics Inc., Dunedin, FL, USA) and a xenon light source (Ocean Optics Inc.) were used with a fibre-optic cable in a $90^\circ/90^\circ$ angle. We measured reflectance using the program Avasoft 7 (Avantes, Eerbeek, the Netherlands).

Reflectance spectra for each measured region were split into four quantal cone catches representing the four cones used in avian vision, denoted VS (Very Short wavelength), S (Short), M (Medium) and L (Long) using the SPEC package

Table 4.1 Morphological parameters of the wild and domestic long-tailed finch populations

Wild population							
	Mean \pm SE (n)		Difference			F	p
	Male	Female	(%)	(sdu)	Cohen's d		
Wing length	58.87 \pm 0.14 (126)	58.09 \pm 0.18 (80)	1.3	0.46	0.07	12.02	<0.001
Tail length	44.58 \pm 0.31 (122)	42.28 \pm 0.39 (78)	5.2	0.61	0.21	21.67	<0.0001
Tail streamer	80.28 \pm 0.95 (113)	69.86 \pm 1.19 (73)	12.9	0.97	0.98	32.66	<0.0001
Tarsus	15.14 \pm 0.04 (125)	14.92 \pm 0.05 (81)	1.5	0.46	0.02	10.04	0.002
Bill length	10.81 \pm 0.04 (124)	10.70 \pm 0.04 (81)	1	0.3	0.01	4.23	0.041
Bill depth	7.60 \pm 0.04 (47)	7.44 \pm 0.05 (25)	2.6	0.6	0.02	7.1	0.017
Mass	14.16 \pm 0.08 (125)	14.26 \pm 0.11 (79)	0.7	0.12	-0.01	0.59	0.445
Patch size	330.38 \pm 5.65 (58)	280.94 \pm 7.19 (33)	15	1.16	3.89	32.66	<0.0001
Domestic population							
Wing length	61.19 \pm 0.29 (21)	60.39 \pm 0.28 (23)	1.3	0.53	0.18	3.84	0.06
Tail length	47.43 \pm 0.60 (21)	44.61 \pm 0.57 (23)	5.9	0.88	0.64	11.51	<0.005
Tail streamer	83.13 \pm 1.89 (16)	71.74 \pm 1.57 (23)	13.7	1.81	2.63	21.45	<0.0001
Tarsus	15.36 \pm 0.14 (21)	15.27 \pm 0.14 (23)	0.6	0.17	0.02	0.18	0.67
Bill length	11.12 \pm 0.08 (21)	11.06 \pm 0.07 (23)	0.5	0.15	0.01	0.31	0.58
Bill depth	7.73 \pm 0.06 (21)	7.72 \pm 0.05 (23)	0.1	0.06	0.00	0.03	0.87
Mass	15.35 \pm 0.40 (21)	15.54 \pm 0.38 (23)	1.2	0.09	-0.04	0.11	0.74
Patch size	387.56 \pm 10.74 (21)	330.60 \pm 10.26 (23)	14.7	1.38	3.84	14.71	<0.0005

Morphological parameters for males and females (mean \pm SE (n)) of wild and domestic populations.

All measurements given in mm, except badge area (mm²) and mass (g). Difference is shown in percentage (%), standard deviation unit (sdu) and Cohen's d (Cohen 1988; calculated as described by Nakagawa & Cuthill 2007) between males and females of both wild and domestic populations is analysed using ANOVAs.

(<http://www.bio.ic.ac.uk/research/iowens/spec>), in R version 2.7.1 following Hadfield & Owens (2006). The three repeat measurements per region were averaged and these cone catches were transformed into three log contrasts with the L cone catch as the denominator (following Hadfield & Owens 2006). The three log contrasts for each patch separately were analysed using principal components analysis to derive Principal Component 1 (PC1) and Principal Component 2 (PC2).

Repeatability

To test the repeatability of morphological and spectrophotometric measurements, a group of 25 individuals held in the aviaries were measured three times by a single observer (birds were released in between measurements). All morphological measurements were highly repeatable (Lessells & Boag 1987; $F_{2,24} = 10.77-864$; $r = 0.72-0.99$; $p < 0.001$).

Statistics

To test differences between males and females of wild and domestic origin for all morphological and spectrometric measurements, ANOVAs were used. The repeatability of the morphological measurements was also tested with an ANOVA. Univariate and multivariate tests were used to analyse the extent of sexual dichromatism. Discriminant analysis was used to determine the most important factors in sex determination and correlations between all traits. Probability values were not corrected for multiple comparisons (see Moran 2003), as our results showed very low p-values for multiple traits, which is very unlikely to be the result of multiple testing.

Table 4.2 Sexual dichromatism in the wild and captive long-tailed finch populations

Region	Origin	Variance explained	Multivariate test for sex		Univariate test for sex		Sex difference?
		PC1 PC2	Wilks' λ	p	F	p	
Upper mandible	Wild	0.907	0.941	0.021	6.83	0.010	Yes
		0.063			1.08	0.300	No
Crown	Wild	0.982	0.884	0.0004	11.67	<0.001	Yes
		0.016			4.40	0.038	No
Upper mandible	Captive-bred	0.940	0.985	0.678	0.42	0.520	No
		0.047			0.37	0.544	No
Crown	Captive-bred	0.937	0.866	0.026	0.79	0.378	No
		0.057			6.99	0.011	Yes

Variance explained by both principal components (PC1 and PC2) and the results of the multivariate test (Wilks' λ represents a measure of difference between the two means ranging between 0 and 1, with values closer to 0 indicating a larger difference in group means) and univariate tests are shown for two body regions, yellow upper mandible and grey crown (captive-bred: 21 males/23 females; wild: 75 males/56 females).

4.4 Results

Level of Sexual Dimorphism

In the domestic population (Table 4.1), there were no significant differences between males and females in tarsus, bill length, bill depth, wing length and mass. Domestic females did have significantly shorter tails, tail streamers and smaller patch than males. No differences were found in spectral reflectance PC1 for either yellow upper mandible or grey crown (only PC2 differed for the grey crown but this explains very little of the variance; Table 4.2).

In the wild population, females had significantly shorter wings (Table 4.1; Figures 4.1 and 4.2), tarsus and tail than males, as well as shorter tail streamers and smaller black patches. Bill size differed slightly between the sexes but could be a result of multiple tests, only mass did not differ. Spectral reflectance PC1 for the upper mandible and grey crown differed significantly between the sexes (Table 4.2). PC2 did not differ significantly for either the yellow upper mandible or the grey crown. Figure 4.3 illustrates the spectral reflectance for the upper mandible (A) and grey crown (B) for the extreme (highest and lowest) males and females of the wild population, while Figure 4.4 illustrates relative dimorphism in colour space.

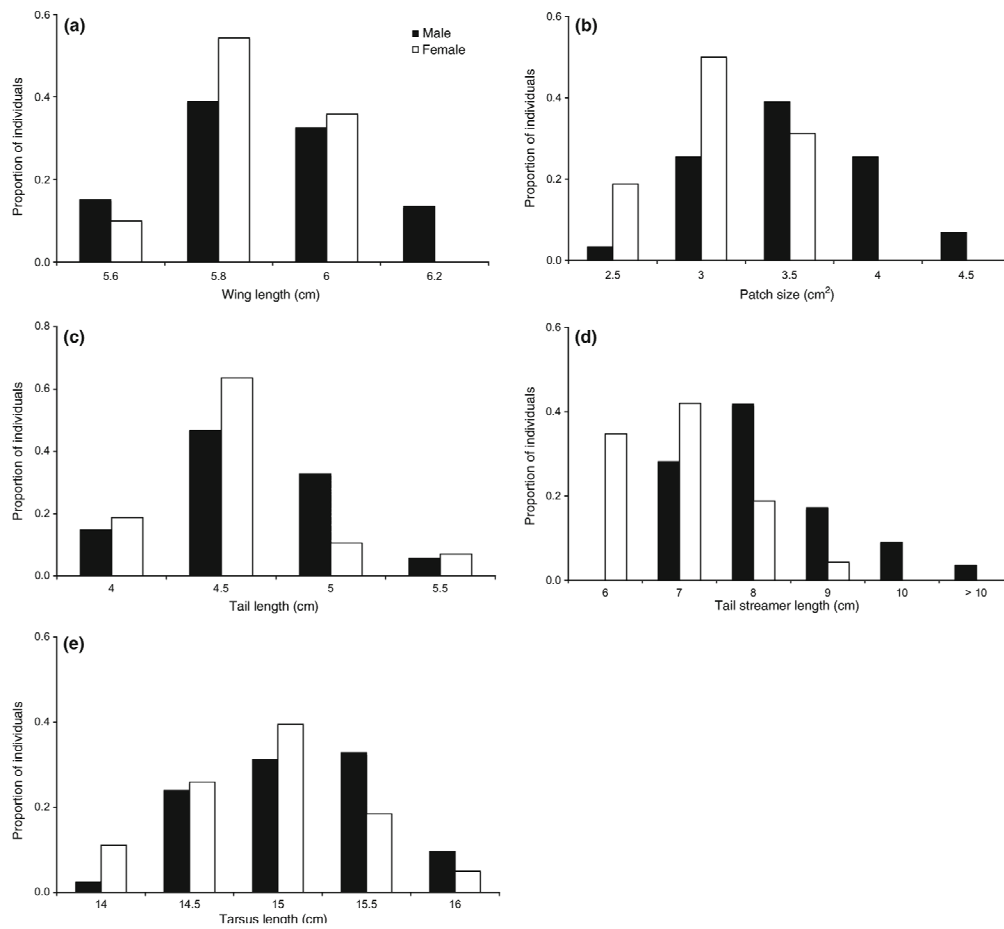


Figure 4.2 Distribution of traits (proportion) for males (black bars) and females (white bars) in the wild population for (a) wing length (male $n = 126$; female $n = 80$), (b) tarsus length (male $n = 125$; female $n = 81$) (c) tail length (male $n = 122$; female $n = 78$), (d) tail streamer length (male $n = 113$; female $n = 73$) and (e) patch size (male $n = 58$; female $n = 33$).

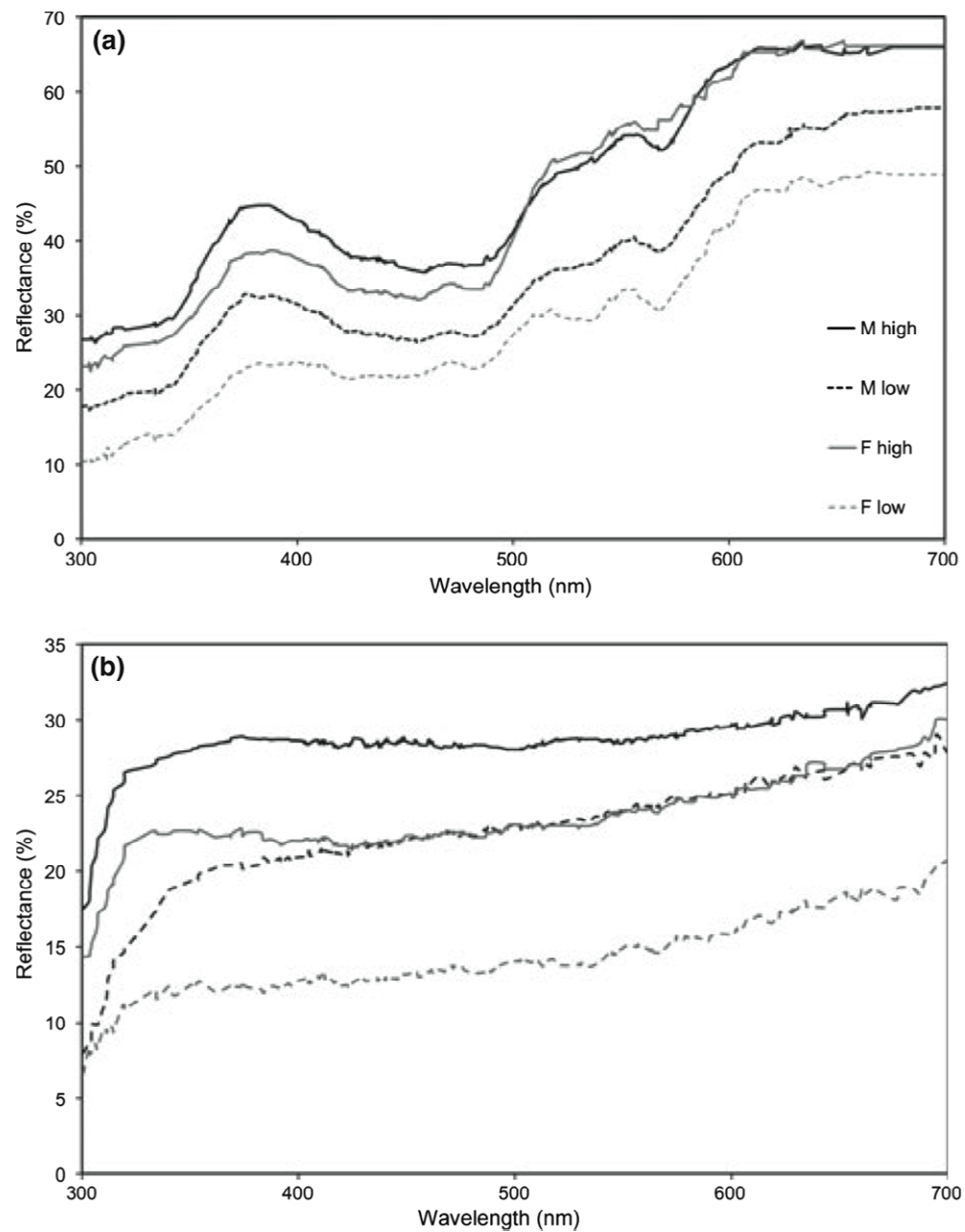


Figure 4.3 Reflectance of upper mandible and grey crown of wild Long-tailed Finches. Highest (black line) and lowest (dashed black line) male and highest (grey line) and lowest (dashed grey line) female for (a) upper mandible and (b) grey crown.

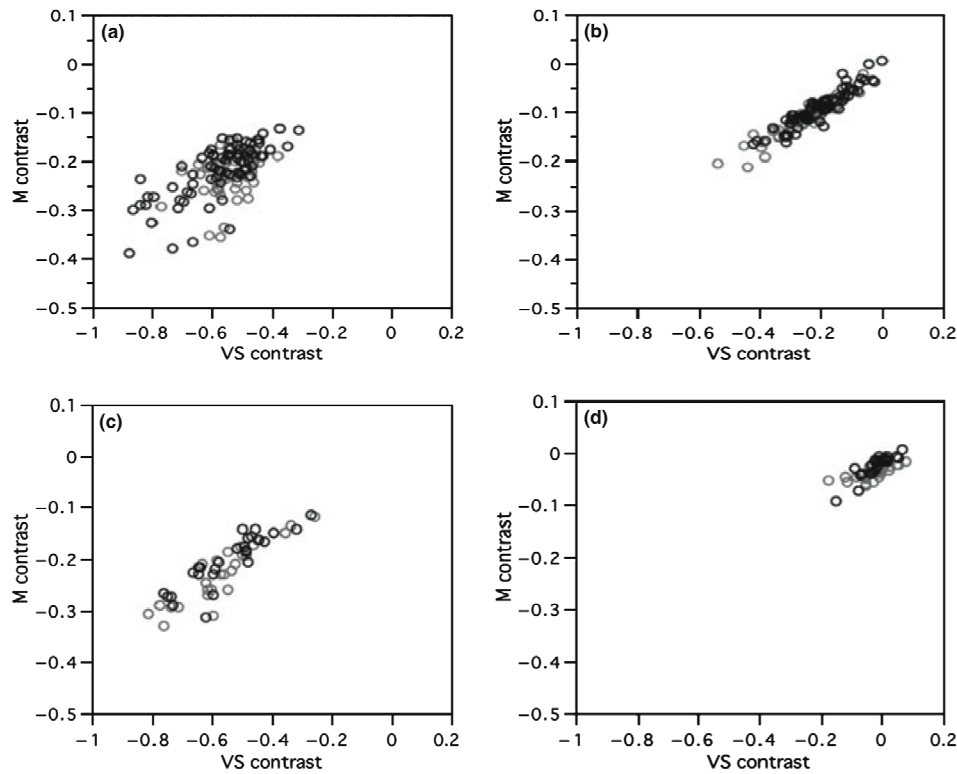


Figure 4.4 Figures illustrating relative dimorphism in colour space across (a) upper mandible wild population, (b) crown wild population, (c) upper mandible captive population, (d) crown captive population (male: black; female: grey). ‘VS and M contrast’ present the contrast in the light stimulating the Very Short Wavelength and Medium Wavelength cones, respectively, with respect to that stimulating the Long Wavelength cones of the passerine eye.

The wild population was sexually dimorphic in seven of ten traits, while the domestic population was sexually dimorphic in only three of ten traits. For all traits, the domestic female distribution is contained entirely within the male distribution, while in the wild population the female distribution overlapped but was not entirely contained within the male distribution (Figure 4.2).

Can Male and Female Long-Tails be Reliably Discriminated?

In the wild population, discriminant analysis correctly predicted the sex of 92% of individuals when all morphological and spectrophotometric parameters were combined (Table 4.3), and only 6% of males were misclassified as female, and 2% of females were misclassified as male. Individually, all traits correctly assign sex between 47.4% and 73.7%, with 11.3–39.3% of males misclassified. Sexual dimorphism was most pronounced in patch size (15% / 1.16 sdu; Table 4.1) and tail streamer length (12.9% / 0.97 sdu). Based on tail streamer and patch size together only 17.7% of males were misclassified (Figure 4.5).

In the domestic population, discriminant analysis showed an 89% correct prediction of sex, when all morphological and spectrophotometric parameters were used (Table 4.3). Only 2.8% of males were misclassified as females. All traits individually correctly assign sex between 47.2% and 79.5%, with 9.1–32.1% of males misclassified. Sexual dimorphism was most pronounced for patch size (14.7% / 1.38 sdu), tail streamer length (13.7% / 1.81 sdu) and tail length (5.9% / 0.88 sdu).

Table 4.3 Discriminant analysis of morphological traits of the wild and captive long-tailed finch populations.

Results of discriminant analysis of all measured traits have been shown to differ significantly between sexes in the wild and captive population. Percentage of individuals for whom sex is assigned correctly, Wilk's k and percentage of males misclassified as female is shown.

	Wild population			Captive population		
	Classified correctly (%)	Wilks' λ	Misclassified males (%)	Classified correctly (%)	Wilks' λ	Misclassified males (%)
Morphological traits						
Tail streamer length	73.7	0.81	11.3	74.4	0.59	15.4
Patch size	70.3	0.69	20.9	79.5	0.73	9.1
Tail streamer & patch size	73.4	0.66	17.7	82.0	0.54	5.1
Tail length	64.0	0.90	11.5	72.7	0.79	15.9
Tarsus length	59.2	0.77	18.4	54.5	0.98	20.5
Wing length	54.4	0.95	39.3	61.4	0.83	27.3
Reflectance						
Upper mandible						
PC1	47.4	0.99	32.1	50.9	1.00	26.4
PC2	52.7	0.97	23.7	47.2	0.98	32.1
PC1 & PC2	51.1	0.97	25.2	47.2	0.98	32.1
Crown						
PC1	59.5	0.96	19.8	60.4	0.99	17.0
PC2	51.9	0.87	25.2	67.9	0.90	11.3
PC1 & PC2	69.5	0.81	13.0	77.4	0.83	7.5
All traits combined	92.0	0.39	6.0	88.9	0.36	2.8
All morphological traits	87.9	0.42	10.3	82.0	0.41	7.7
All reflectance traits	68.7	0.78	12.2	77.4	0.82	7.5

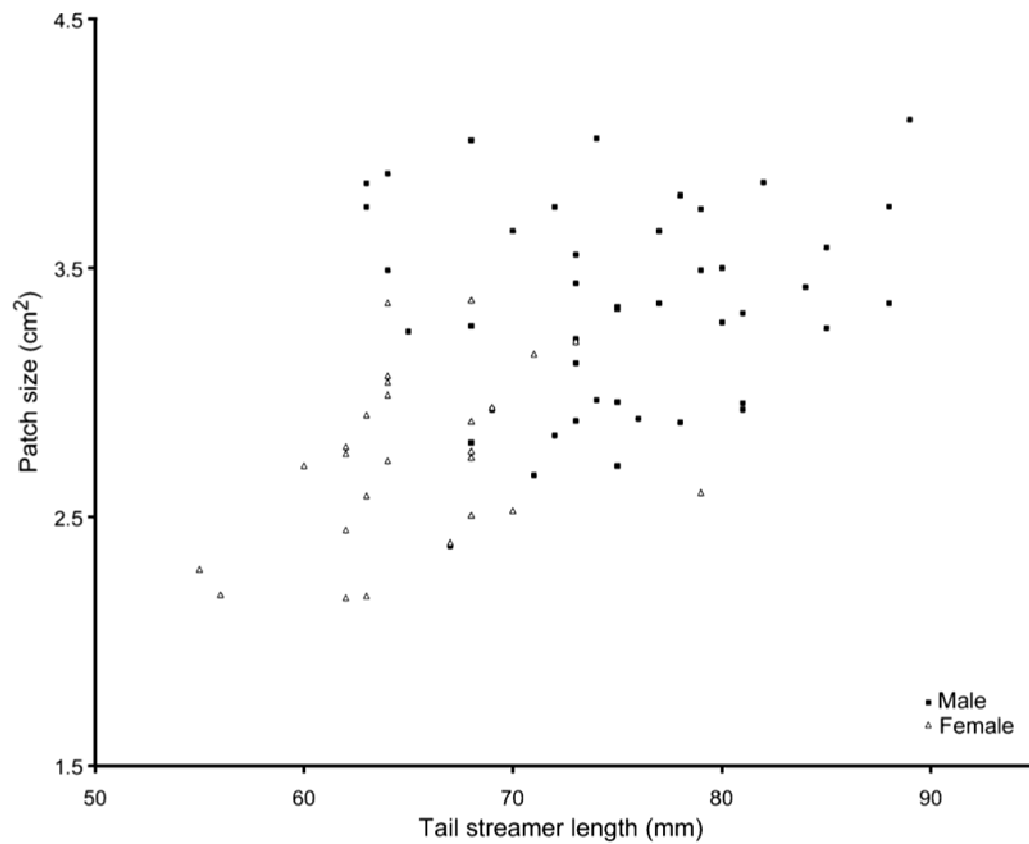


Figure 4.5 Patch size and tail streamer length of 26 females and 44 males of the wild population (males black diamonds; females open triangles). About 18% of males lie in a zone of overlap between the sexes and could belong to either sex based on these two parameters.

4.5 Discussion

Since the sexual indistinguishability hypothesis was first published (Burley 1981), the importance of the differences between avian and human vision has been demonstrated (Bennett *et al.* 1994). We now know that birds, unlike humans, can distinguish reflectance in the UV spectrum and have tetrachromatic vision, which affords them better colour vision than our own trichromatic vision. The use of optical spectrometry to objectively assess the expression of colour in birds, and the true level of dichromatism has greatly improved the ability to assess monomorphism in bird species. Based on these methods, often subtle but significant sexual dichromatism has been shown in several species that were previously believed to be monomorphic e.g. starlings *Sturnus vulgaris* (Cuthill *et al.* 1999) and whistling thrush *Myiophonus caeruleus* (Andersson 1999). Therefore, many other apparently monomorphic species are likely to be dichromatic on closer investigation.

To date, the long-tailed finch provides the only solid support (Langmore & Bennett 1999) for the sexual indistinguishability hypothesis (Burley 1981). The long-tailed finch has previously been described as sexually monomorphic (Immelmann 1965; Langmore & Bennett 1999), but this was based on observations from a) wild birds before the advent of new and sensitive quantitative techniques for measuring colour, or b) the measurement of domesticated individuals that have been kept in captivity for many generations. Santos & Lumeij (2007), however, later classified this species as sexually dichromatic with respect to bill and crown. Combining morphological and spectrophotometric measurements in a wild population, our results demonstrate that while male and female long-tailed finches are similar, they are not completely sexually monomorphic.

The wild population is sexually dimorphic in seven of ten traits and the female distribution is not entirely contained within the male distribution for all traits. Across individual traits, males were slightly larger with respect to wing (1.3%) and tarsus length (1.5%), with a more pronounced level of dimorphism in three putative sexually selected ornamental traits, patch size (15%), tail streamer length (12.9%) and tail length (5.2%). Males were also slightly more chromatic in the expression of colour of both the yellow upper mandible and grey crown. Only body mass and bill size did not differ between the sexes in the wild population. The domestic population, however, was found to be sexually dimorphic in only three of the ten traits, and the female distribution was contained entirely within the male distribution. The sexes differed in patch size (14.7%), tail streamer length (13.7%), tail length (5.9%), but not in spectral reflectance of upper mandible and crown. These differences are similar to those demonstrated by Langmore & Bennett (1999) for the domesticated population they studied in the United Kingdom. While it is difficult to draw a clear conclusion on the comparison between a single domestic and wild population, it is certainly possible that there may be a difference in the level of sexual dimorphism in domestic and wild birds. In the zebra finch (*Taeniopygia guttata*), recent studies have suggested that domesticated birds are different from wild birds in both morphological and behavioural traits (e.g. Rutstein *et al.* 2007), probably as a result of the artificial selection imposed on birds by aviculturists. However, the difference in the degree of sexual dimorphism in the domestic and wild populations reported here is relatively minor, with the key point being that in the wild, if anything the level of sexual dimorphism is greater than found in previous studies of domestic birds.

Although there is overlap in individual traits between the sexes in the long-tailed finch, the main question with regard to Burley's (1981) sexual indistinguishability hypothesis is whether males and females can be distinguished with a degree of confidence. Many studies of ornamentation, signalling and sexual selection have focused on single conspicuous traits (e.g.

collared flycatcher *Ficedula albicollis* Griffith & Sheldon 2001), but most species possess multiple complex ornaments that are displayed by one or both of the sexes and are important in signalling different qualities (Pryke *et al.* 2001, 2002; Pryke & Andersson 2005). The expression of several traits by the long-tailed finch (tail streamers, coloured bill, black throat patch), which all might have a signalling function, and the demonstration of multiple signalling in other species, means that it is appropriate to account for all of them simultaneously in any investigation into sexual signalling.

Our analysis, using just ten morphological traits, demonstrated that over 90% of individuals in the wild population could be reliably sexed on the basis of appearance alone. Furthermore, based on this analysis, only 6% of males in this population were mistaken for females, which provide only a very small group of males the opportunity to conceal their sex in the absence of behavioural cues. Although without a full understanding of the cognitive system of the long-tailed finch, it is difficult to know with certainty, it seems likely that individuals are able to discriminate sex with a higher level of accuracy given that they will also use a number of other morphological traits not measured here and may be able to discriminate finer levels of variation than we were able to with our tools. In addition to the morphological traits that we have analysed here, in a natural situation, individuals will receive further potentially useful information through behavioural and acoustic cues that are received over long-term interactions with other individuals in this flock-living species.

Interestingly, despite the level of sexual dimorphism that we have demonstrated in this species, Langmore & Bennett (1999) did find that males courted both unfamiliar males and females but not as often familiar males. It is possible that the males knew that they were courting other males, but did so as part of establishing a dominance hierarchy, or they were confused as to the sexual identity of the unknown individuals they were exposed to in that

experiment. However, we do not agree that this necessarily implies that in a natural context there will be any confusion. First, as we have shown the sexes are easier to discriminate in the wild (than in the domestic population) because of the greater degree of sex-dependent variation in the various morphological traits measured. Second, the effects noted by Langmore & Bennett (1999) occurred during the first 15 min that individuals came into contact with one another in a highly unnatural and presumably quite stressful context (they increased the level of stress by reducing the size of the cage and providing only limited access to a favoured food source). By contrast, our work on a wild population suggests that this species is highly sedentary and lives in relatively small and fairly stable social groups throughout the year. For example, 45% of the breeding adults in the breeding area in 2009 had been banded while breeding in the same area in 2008 and most adults bred at a nest site within 1 km of that used in the previous year. The adults in each of the small populations we studied would therefore have had prolonged contact with other members of the flock at feeding and watering sites throughout the year. Therefore, while it is possible that on a quick visual inspection the sexes may be difficult to determine, in an appropriate ecological context it is difficult to see that concealing one's sex is either possible or adaptive.

Using quantitative measures of colour and a discriminant function analysis, we have demonstrated that while the level of sexual dimorphism across a number of traits is limited, together these characters are sufficient to accurately signal the sex of an individual. The same approach has produced similar results in other species e.g., spotted bowerbirds *Chlamydera maculata* (Madden *et al.* 2004) and crested auklets *Aethia cristatella* (Jones 1993). Given our results in the long-tailed finch, which has been the focus of previous work, and these other species, we believe that it is unwise to classify any species as being truly sexually monomorphic (and the sexes indistinguishable) until a thorough analysis has accounted for all the subtle variation in the expression of colour, the multiple traits that may be involved and

finally a consideration of the appropriate ecological context in which these may have evolved.

We suggest that the sexual indistinguishability hypothesis (Burley 1981) does not account for the similarity between males and females in this species. This now provides an interesting challenge of why the males and females of this, and many other species, are morphologically very similar, whereas in many other ecologically similar and phylogenetically related species, the expression of sexual dimorphism is readily apparent, and often the female express no ornamental traits at all (Clutton-Brock 2009). The expression by female long-tailed finches of all of the ornamental plumage traits displayed by males, but to a slightly lesser extent, raises interesting questions about the role of sexual selection on females in this species and the potential for mutual mate choice.

4.6 Acknowledgements

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CHAPTER FIVE

No evidence for assortative mating
on the basis of putative ornamental traits



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5.1 Abstract

When multiple ornaments are expressed in both sexes, they are assumed to be maintained by mutual sexual selection and function in mate choice. In the Long-tailed Finch *Poephila acuticauda* both sexes exhibit multiple putative ornaments that vary in their expression in either size (pintail and throat patch) or colour (bill) between individuals and sexes. We investigated whether these putative ornaments are maintained by mutual sexual selection by exploring whether individuals in a wild population paired assortatively with respect to these ornamental traits, body size and body condition. In addition we explored the degree to which the expression of these putative ornamental traits were indicative of reproductive success.

We did not find clear evidence of assortative pairing with respect to variation in homologous putative ornaments, or body condition in the two sexes, although we did find some quite weak assortative pairing on the basis of wing length. In addition, we found no effect of ornament expression on the reproductive success of either males or females.

Our findings suggest that the expression of these apparently ornamental traits in both sexes of this species may play no current role in mutual mate selection, or as indicator traits of reproductive performance. We are currently unable to identify any function for these very elaborate ornaments in either sex of this species and suggest that the typical assumption that all such traits have an ornamental function may need further examination.

5.2 Introduction

Ornamental secondary sexual traits are widespread throughout the animal kingdom and are well exemplified in birds with many species exhibiting elongated tails, and/or highly coloured plumage or legs, feet and bills whose expression far exceeds any obvious naturally selected purpose with respect to, for example, aerodynamics or crypsis. Typically, elaborate or extravagant traits in males are assumed to result from intra- or inter sexual selection (Andersson 1994), targeting good quality individuals through the expression of a condition dependent trait (Andersson 1986; Grafen 1990). Empirical work to date across many taxa has found support for this earlier theoretical work, however a number of important questions have been largely neglected or remain generally unresolved. For example, relatively few studies have investigated the role of putatively ornamental traits in species in which the expression of the trait is approximately equal in males and females (Kraaijeveld *et al.* 2007; Clutton-Brock 2007, 2009). Whilst we know that the level of sexual dimorphism in a species is related to things such as the level of extra-pair paternity in a species (e.g. Owens & Hartley 1998), it is not always clear why some species have a high level of sexual dimorphism and other closely related species are sexually monomorphic (reviewed by Amundsen 2000 and Clutton-Brock 2009). It has been proposed that the elaborate mutual characters are functional only in males with female expression the result of shared genetic architecture (genetic correlation hypothesis; Lande 1980; Lande & Arnold 1985). However, ornamental traits might also be expressed in females due to direct selection on females (Darwin 1871; Johnstone *et al.* 1996), if they have a signaling function in both sexes and are favoured by mutual sexual selection driven by both female and male competition for mates (e.g. Jones & Hunter 1993; Romero-Pujante *et al.* 2002; Kraaijeveld *et al.* 2004).

If both sexes have the same preferences in mate ornament expression this may result in assortative mating with respect to ornament expression, with individuals of similar phenotype mating together more frequently than expected by chance (Burley 1983). In monogamous species, male reproductive success will be largely dependent on the fecundity of their female partner and males should therefore also be choosy about their social partner (Johnstone *et al.* 1996; Amundsen 2000; Kokko & Monaghan 2001). Therefore, assortative mating might arise via mutual male and female preferences for the same selection criteria, where although all individuals attempt to gain a mate of the highest quality, those of low quality are competitively constrained in mate choice (Johnstone *et al.* 1996).

Assortative mating is well documented in many bird species and may occur by body size (e.g. Delestrade 2001; Moreno-Rueda 2005), wing length (e.g. Moreno-Rueda 2005; Komdeur *et al.* 2005), tarsus (Delestrade 2001), bill depth (Wagner 1999), tail length (e.g. Johnstone *et al.* 1996; Boland *et al.* 2004) and body condition (Bortolotti & Iko 1992). Assortative mating based on age is also often found, as morphological characters may change with age (e.g. Komdeur *et al.* 2005). Positive assortative mating also occurs based on ornaments, like crown UV (Andersson *et al.* 1998), bill and plumage colour (Jawor *et al.* 2003), patch size (Masello & Quillfeldt 2003) and other plumage ornaments (e.g. Kraaijeveld *et al.* 2004).

In the socially monogamous passerine, the Long-tailed Finch (*Poephila acuticauda*), both sexes possess multiple ‘putative ornamental traits’ (hereafter ornaments) - two long pintail feathers, a black throat patch and in western populations, an orange-yellow coloured bill. This species is typically described as sexually monomorphic (Higgins *et al.* 2006), but qualitative examination reveals a slight degree of dimorphism in ornament expression, with males having longer tails and larger throat patches than females and being slightly different in the expression of bill colour (Van Rooij & Griffith 2010). All of these ornamental traits have a

degree of variation in their expression within each sex suggesting that they might be capable of signaling variation in individual quality. In this species pair bonds are very strong and appear to last until the death of one member of the pair (Zann 1977; Van Rooij & Griffith In Press), which makes initial pair formation very important. Both partners also contribute substantially to incubation and provisioning of the brood and therefore this species has all the characteristics of a species in which mutual mate choice is predicted (Trivers 1972; Johnstone *et al.* 1996; Kokko & Johnstone 2002).

Here, in a wild population of Long-tailed Finches, we investigated whether positive correlations exist within pairs between these different sexual ornaments (pintail length, patch size and bill colour), body size and body condition, i.e. whether this species mates assortatively with respect to ornament expression and body size and condition. Further, we assessed whether the expression of ornaments is indicative of reproductive success.

5.3 Methods

Fieldwork and Study Species

Long-tailed Finches were studied during their breeding season between February and September from 2008 to 2010 in the Eastern Kimberley, near Wyndham, Western Australia (S15°33'38", E128°08'59") as part of an ongoing study. The Long-tailed Finch is a common Australian grass finch (family Estrildidae), endemic to the savanna woodland of tropical northern Australia (Immelmann 1965; Higgins *et al.* 2006). Both sexes participate in nest construction, incubation, brooding and feeding of the altricial nestlings (Immelmann 1965; Higgins *et al.* 2006; EP van Rooij, pers. obs.). Long-tailed Finches have a fawn/brown body, blue-greyish head, black throat patch, black tail and long black tail streamers. Visually, they

appear to be sexually monomorphic, but a more quantitative assessment reveals significant sex differences in the expression of tail streamer length, patch size and bill and head colour, although there is considerable overlap between males and females in all traits (Van Rooij & Griffith 2010).

During the breeding season, nesting individuals were caught either on their nest with handnets or near their nest with mistnets at waterholes. All birds were banded with a metal band and individual combinations of colour bands. Pair identity - the only two birds that fed at that nest - was confirmed by nest watches during chick feeding.

Morphological and spectrophotometric measurements

Upon capture a blood sample (<20µl) was taken from the brachial vein (wing) of adult birds and used to reliably determine their sex with the molecular sex markers P2 and P8, a well-established technique (Griffiths *et al.* 1998) and used reliably in this species before (Van Rooij & Griffith 2010).

The degree of assortative mating was assessed across a number of morphological traits. Tarsus, bill, tail and pintail length (to the nearest 0.1mm), wing (to the nearest 0.5mm) and body mass (to the nearest 0.1 g) were measured. Patch size was measured from photos of each individual in the exact same posture, restrained in an artificial holder with the head tilted back. The number of pixels of the patch was then measured using the freehand selections tool and area measure option in the program ImageJ (Version 1.40G). Since the distance at which the picture was taken (approx. 20cm) was not constant, a ruler was attached to the bird holder to allow accurate comparison between pictures (for detailed methods see Van Rooij & Griffith 2010). Spectral reflectance of the upper mandible was measured in three consecutive

scans taken from the centre of the bill. A USB2000+ Miniature Fiber Optic spectrophotometer (Ocean Optics Inc., Dunedin, USA) and a xenon light source (Ocean Optics Inc., Dunedin, USA) were used with a fiber-optic cable in a 90°/90° angle. We measured reflectance using the program Avasoft 7 (Avantes, Eerbeek, the Netherlands); for detailed methods see Van Rooij & Griffith (2010). Reflectance spectra for each measured region were split into four quantal cone catches representing the four cones used in avian vision, denoted VS (Very Short wavelength), S (Short), M (Medium) and L (Long) and summarized into one Principal Component (PC1; explaining 94% of variation in this population), again further details are given in Van Rooij & Griffith (2010).

We also computed a body condition index as the residuals from a linear regression of body mass on tarsus length as is commonly used (e.g. Ots *et al.* 1998). We calculated a body size PC by summarizing tarsus length, bill length and wing length into one Principal Component performed on unscaled data (99.9 explained by PC1; 0.24 explained by tarsus length; 0.95 by wing length; 0.17 by bill length). Throughout each breeding season (March to August), we continuously monitored all breeding activity in the population and scored clutch size and number offspring fledged per attempt.

Analysis

Data were not normally distributed; therefore non-parametric tests were used throughout. A Bonferroni correction was used when comparing multiple traits to control for Type I error. Power of all analyses was assessed with G*Power 3.1 (Faul *et al.* 2007). Spearman correlations were used to assess assortative mating by body size, condition and ornament expression in several ways: (1a) all pairs n=89; (1b) only 2008 n=42; (1c) only 2009 n=29;

(1d) only 2010 n=18; (2) newly formed pairs for each year (individuals who bred with a different partner the previous season or earlier in the same season; n=24).

Reproductive success was assessed in several ways: (a) Spearman correlations were used to assess if two measures of reproductive success (clutch size and number of offspring fledged) were correlated with male and female morphology, condition and ornamentation for all breeding attempts (n=89) (b) Given the fact that individual females/males may prefer different males/females we looked at whether females/males in a certain condition or a certain expression of ornamentation preferred specific individuals (Griggio & Hoi 2010) or differed in reproductive success. Therefore, individuals were grouped by body size, condition and ornament expression (SPSS visual binning method all data grouped in four groups: 1: lowest - 1stdev below mean, 2: 1stdev below mean – mean, 3: mean - 1stdev above mean, 4: 1stdev above mean - highest) and compared with ANOVA with respect to reproductive success (clutch size and number of offspring fledged) and their mate preference; (c) pairs were grouped based on reproductive success (clutch size and number of offspring fledged; SPSS visual binning method all data grouped in four groups: 1:lowest - 1stdev below mean, 2: 1stdev below mean – mean, 3: mean - 1stdev above mean, 4: 1stdev above mean - highest) and with ANOVAs the corresponding morphology, condition and ornament expression were assessed; (d) To investigate the effect of the similarity of male and female ornamentation within a pair, the effect of pair asymmetry (% difference between male and female) in ornament expression were correlated with reproductive success (clutch size and number of offspring fledged) and pair asymmetry was grouped and compared with reproductive success with ANOVAs.

Table 5.1 Sexual dimorphism

Bonferroni correction for multiple testing lowers α to 0.006.

	Male				Female				Sex difference			
	mean	se	%CV	n	mean	se	%CV	n	%	CV	F	p
Mass	14.42	0.84	5.83	88	14.17	0.86	6.07	81	1.73	5.98	3.83	0.520
Tarsus	15.16	0.46	3.03	88	14.96	0.47	3.14	82	1.32	3.14	7.77	0.006**
Wing	59.09	1.65	2.79	88	58.18	1.35	2.32	82	1.54	2.69	15.25	0.000**
Bill	10.77	0.44	4.09	88	10.73	0.41	3.82	82	0.37	3.96	0.38	0.540
Tail	46.57	4.15	8.91	88	43.96	2.57	5.85	82	5.60	8.17	23.85	0.000**
Pintail	83.22	10.77	12.94	88	71.28	8.8	12.35	81	14.35	14.87	61.56	0.000**
Patch size	340.1	46.04	13.54	40	279.4	36.9	13.24	38	17.85	16.62	40.94	0.000**
Bill PC	0.98	0.26	26.53	31	1.08	0.39	36.11	30			1.50	0.226

* significant $p < 0.05$, ** significant after Bonferroni correction $p < 0.006$

Table 5.2 Correlates of expression of putative ornaments, body measures and body condition within the sexes.

Correlations of morphological measures within males (top right above diagonal) and within females (bottom left under diagonal). Ornaments (pintail length, patch size and bill PC), body size (wing, tarsus) and body condition (residual of linear regression of body mass on tarsus). N is lower for patch size and bill colour PC as these have not been measured for all individuals. Bonferroni correction for multiple testing lowers α to 0.007.

		Male Body measure correlations					
		Tarsus	Wing	Body condition	Body size	Pintail	Patch
Female Body measure correlations	rs		0.012	-0.135	0.145	-0.104	0.010
	p		0.909	0.211	0.178	0.337	0.953
	n		88	88	88	88	40
	rs	0.107		0.208	0.985**	0.274*	0.266
	p	0.340		0.052	0.000	0.010	0.097
	n	82		88	88	88	40
	rs	0.037	-0.073		0.199	0.031	0.050
	p	0.745	0.516		0.063	0.776	0.761
	n	81	81		88	88	40
	rs	0.281*	0.975**	-0.073		0.275*	0.257
	p	0.010	0.000	0.518		0.010	0.110
	n	82	82	81		88	40
	rs	-0.131	-0.049	0.028	-0.083		0.247
	p	0.244	0.667	0.809	0.460		0.124
	n	81	81	80	81		40
	rs	-0.100	-0.023	0.325*	-0.033	0.131	
	p	0.552	0.891	0.047	0.844	0.440	
	n	38	38	38	38	37	
	rs	-0.276	-0.208	-0.294	-0.179	-0.221	-0.039
	p	0.139	0.271	0.114	0.345	0.240	0.870
	n	30	30	30	30	30	20

* significant $p < 0.05$, ** significant after Bonferroni correction $p < 0.007$

Table 5.3 Morphology of breeding and non-breeding individuals and individuals breeding early or late.

Comparison of morphology of non-breeding individuals with breeding individuals (breeding males n=89; females n= 82; non-breeding males n=82; females n=40) with t-tests and comparison of individuals breeding early in the season with individuals breeding only late in the season (early breeders males/females n=39; late breeders males/females n=36) with t-tests.

		Breeding vs non-breeding		Breeding early vs late	
		M	F	M	F
Tarsus	t	-0.165	-1.957	-0.089	-0.261
	p	0.869	0.053	0.930	0.794
	n	170	117	75	75
Wing	t	-0.620	1.140	-0.346	0.789
	p	0.536	0.257	0.730	0.432
	n	171	117	75	75
Body Condition	t	-1.327	0.366	0.483	-0.666
	p	0.186	0.715	0.630	0.508
	n	147	116	75	75
Body size	t	-0.522	0.879	-0.380	0.734
	p	0.602	0.381	0.705	0.465
	n	169	117	75	75
Pintail	t	-1.432	-0.689	0.079	-0.136
	p	0.154	0.492	0.938	0.892
	n	151	105	75	74
Patch size	t	-0.791	0.192	-0.461	-0.157
	p	0.431	0.848	0.647	0.876
	n	85	58	40	38
Bill colour	t			-0.266	-0.809
	p			0.792	0.424
	n			33	32

As the data on assortative mating only considers breeding birds, it is possible that these findings do not reflect the variation seen in ornaments across the wider population. Therefore we investigated the possibility that non-breeding birds are consistently different from the breeding birds in two ways. We compared the morphology of breeders with individuals, which were caught at water holes but were never observed breeding. Second, we consider that the birds that only started breeding in the second half of the breeding season were floaters or non-breeders during the first half of the season and therefore have compared individuals breeding in the first half of the season to individuals that only bred during the second half of the breeding season.

5.4 Results

During three consecutive breeding seasons (2008-2010) 97 breeding pairs were recorded (44 pairs in 2008; 33 pairs in 2009 and 20 pairs in 2010). For pairs that bred during more than one season (eight pairs) only the first recorded breeding attempt was included and the second was excluded from analysis, therefore 89 unique pairs were used for the analysis (42 pairs in 2008; 29 pairs in 2009 and 18 pairs in 2010). Long-tailed Finches are slightly sexually dimorphic, with most variation in pintail length and patch size within and between the sexes (Table 5.1). Within individuals there were some correlations between the expression of different traits; in males wing length, body size and pintail length were correlated (Table 5.2; above diagonal), while in females patch size correlated with body condition (Table 5.2; under diagonal). We found no difference between the breeding and non-breeding birds ($t < 1.14$, $p > 0.053$; Table 5.3), or early and late breeders with respect to any of the traits examined ($t < 0.789$, $p > 0.424$; Table 5.3) and therefore believe that the following results, based on just the breeding birds are representative of the population wide expression of traits.

Table 5.4 Correlations of female and male trait expression.

Correlations of female and male body measures, body condition and ornaments within pairs. N is lower for patch size and bill colour PC as these have not been measured for all individuals. Some values are missing due to a too small sample size. Bonferroni correction for multiple testing lowers α to 0.007. Average power is 0.26 (0.05 – 0.71).

		tarsus length	wing length	body condition	body size	pintail length	patch size	bill colour PC
New pairs	rs	0.264	0.252	-0.180	0.267	-0.056	-0.523	0.157
	p	0.213	0.234	0.423	0.207	0.793	0.229	0.711
	n	24	24	22	24	24	7	8
New pairs in experiment	rs	0.100	-0.553		-0.700	0.553		
	p	0.873	0.334		0.188	0.334		
	n	5	5		5	5		
All pairs 2008-2010	rs	0.031	0.207	-0.040	0.167	-0.017	-0.331	-0.176
	p	0.770	0.052	0.712	0.117	0.872	0.099	0.371
	n	89	89	89	89	88	26	28
2008	rs	0.079	0.347*	0.107	0.370*	-0.071	-0.800	-0.400
	p	0.620	0.024	0.499	0.016	0.660	0.200	0.505
	n	42	42	42	42	41	4	5
2009	rs	-0.268	0.117	-0.266	0.125	0.176	0.028	-0.115
	p	0.160	0.545	0.163	0.519	0.361	0.925	0.600
	n	29	29	29	29	29	14	23
2010	rs	0.372	-0.080	-0.008	-0.051	-0.252	-0.667	
	p	0.129	0.751	0.974	0.842	0.313	0.071	
	n	18	18	18	18	18	8	

* significant $p < 0.05$, ** significant after Bonferroni correction $p < 0.007$

Assortative mating

When taking only newly formed pairs into account (individuals who bred with a different partner the previous season or earlier in the same season; $n=24$) there were no correlations within pairs for expression of any of the putative ornamental traits between males and females (Table 5.4). However, when all pairs (2008-2010) were assessed together a trend was found for a correlation between male and female wing length ($r_s=0.207$, $p=0.052$, $n=89$) and a very weak negative trend for patch size ($r_s=-0.331$, $p=0.099$, $p=26$), although neither result was significant when correcting for multiple testing (Table 5.4). When analysing the correlations between pairs separately for 2008 (Table 5.3) wing length ($r_s=0.347$, $p=0.024$, $n=42$) and body size ($r_s=0.370$, $p=0.016$, $n=42$) were correlated within pairs (but not after the Bonferroni correction), in 2009 none of the traits correlated between males and females (Table 5.4) and in 2010 there was a trend for a correlation of male and female patch size ($r_s=-0.667$, $p=0.071$, $n=8$; Table 5.4), although not after correcting for multiple testing.

When all paired individuals were grouped into four categories based on the different traits, male and female categories correlated for wing length ($r_s=0.228$, $p=0.031$) and bill colour ($r_s=-0.388$, $p=0.041$) and showed a positive trend for body size ($r_s=0.198$, $p=0.063$) and a negative trend for patch size ($r_s=-0.338$, $p=0.091$), although not after correcting for multiple testing.

Table 5.5 Male and female body measures and ornament expression and reproductive success.

Spearman correlations were used to compare body size (tarsus and wing length), body condition and ornament expression (pintail length, patch size and bill colour PC) with reproductive success (clutch size, number offspring fledged per attempt). Body measures were grouped in four categories and reproductive success was compared (with ANOVAs) between largest and smallest individuals. N is lower for patch size and bill colour PC as these have not been measured for all individuals. Bonferroni correction for multiple testing lowers α to 0.007. Average power is 0.18 (0.05 – 1.00).

		Clutch size					Number fledged				
		rs	p	n	F	p	rs	p	n	F	p
Tarsus	Male	0.028	0.814	75	0.286	0.836	-0.125	0.351	58	0.468	0.706
	Female	-0.034	0.771	75	0.235	0.872	-0.077	0.564	58	0.457	0.713
Wing	Male	0.146	0.210	75	1.366	0.260	0.266*	0.044*	58	2.019	0.122
	Female	-0.043	0.711	75	0.886	0.453	0.046	0.734	58	0.095	0.962
Body condition	Male	-0.011	0.923	75	0.324	0.808	0.207	0.119	58	1.899	0.141
	Female	-0.030	0.801	75	3.067	0.033*	0.127	0.341	58	2.141	0.106
Body size	Male	0.136	0.244	75	2.370	0.078	0.247	0.062	58	1.467	0.234
	Female	-0.065	0.580	75	0.919	0.436	0.036	0.789	58	0.227	0.877
Pintail	Male	0.086	0.461	75	1.633	0.189	0.789	0.982	58	0.742	0.532
	Female	0.132	0.261	74	0.405	0.750	0.117	0.387	57	0.733	0.537
Patch size	Male	0.216	0.174	41	0.090	0.965	0.093	0.608	33	0.226	0.878
	Female	-0.045	0.783	39	0.329	0.804	-0.002	0.991	30	0.042	0.988
Bill colour PC	Male	-0.125	0.468	36	0.430	0.733	0.059	0.754	31	0.023	0.995
	Female	0.026	0.881	35	0.332	0.802	-0.013	0.945	32	0.311	0.817

* significant $p < 0.05$, ** significant after Bonferroni correction $p < 0.007$

Ornament expression and reproductive success

Expression of female ornamentation, body size or condition did not correlate with clutch size (Table 5.5). Male ornament expression, body size and condition did not correlate with the clutch size of the female they were paired with (Table 5.5). Again, when body measures were grouped in four categories clutch size was related to female body condition ($F_{3,74}=3.067$, $p=0.033$), but this was not driven by differences between the females in lowest and highest condition (post hoc $p=1.0$) and for male body size ($F_{3,74}=2.370$, $p=0.078$), but not between the smallest and largest males (post hoc $p=1.0$) and not after correcting for multiple testing.

The number of fledged offspring was affected by male wing length ($r_s=0.266$, $p=0.044$) and male body size ($r_s=0.247$, $p=0.062$), but and not after correcting for multiple testing (Table 5.5). When body measures were grouped in four categories there was no difference in clutch size or number of fledged offspring for any of the body measures (Table 5.5).

When reproductive success (clutch size and number of offspring fledged) was grouped into four categories (Table 5.6) reproductive success did not differ for male and female ornament expression, body size and condition, only male pintail differed with clutch size of the female he was paired with ($F_{3,74}=3.981$, $p=0.011$), but not between smallest and largest clutches (post hoc $p=1.0$) and not after correcting for multiple testing.

Table 5.6 Reproductive success (clutch size and number of offspring fledged) grouped into four categories. Body measures of males and females were compared for pairs with high and low reproductive success. Bonferroni correction for multiple testing lowers α to 0.007.

		Clutch size			Number fledged		
		F	p	n	F	p	n
Tarsus	Male	0.445	0.722	75	0.371	0.262	58
	Female	0.308	0.819	75	0.173	0.914	58
Wing	Male	0.604	0.614	75	1.452	0.238	58
	Female	1.401	0.250	75	0.895	0.450	58
Body condition	Male	0.384	0.765	75	0.606	0.614	58
	Female	0.799	0.498	75	1.606	0.199	58
Body size	Male	0.556	0.646	75	1.382	0.258	58
	Female	1.465	0.231	75	0.889	0.453	58
Pintail	Male	3.981	0.011*	75	0.773	0.514	58
	Female	0.715	0.547	74	3.068	0.036*	57
Patch size	Male	0.544	0.655	41	0.983	0.414	33
	Female	0.805	0.499	39	1.198	0.330	30
Bill colour PC	Male	0.695	0.562	36	0.630	0.602	31
	Female	0.296	0.828	32	1.025	0.396	32

* significant $p < 0.05$, ** significant after Bonferroni correction $p < 0.007$

5.5 Discussion

In this study, in a wild population of Long-tailed Finches, we assessed whether pairs mated assortatively based on putative ornamental traits, body size and condition and whether these traits signified reproductive success. When accounting for all the pairs that bred over the years (2008-2010) a trend for assortative mating by wing length and patch size was apparent, but was not consistent across different years, and no trait was consistently correlated across pair members, nor strongly correlated in any single year. Assortative mating in this larger sample may be obscured by the expression of traits in pairs that were formed in previous years. However, in newly formed pairs (where assortative mating should be easier to detect) we found no positive correlations between the different putative ornamental traits (pintail length, patch size and bill colour), body size and condition expressed by the male and female of a pair, i.e. individuals did not mate assortatively based on expression of these putative ornaments, body size or condition. Furthermore, neither male nor female ornament expression, body size or condition predicted reproductive success (clutch size and number of offspring fledged). Only male wing length was correlated with the number of offspring fledged (although this weak correlation did not hold after correcting for multiple testing).

Assortative mating by mutual mate choice might not be possible because of a constrained choice of mates, i.e. although both male and female would like to select mates based on ornament expression the preferred partner is not available at the time of choosing, therefore this preference does not result in an assortative mating pattern. The number of available partners in this population might be limited because Long-tailed Finches remain paired across seasons and form long-term pair bonds, thereby restricting the mating pool to individuals that were previously unpaired, were divorced, or whose mate had died. We did examine the possibility that the non-breeding birds were different from the breeding birds but found no

difference with respect to any of the ornamental or morphological traits examined, suggesting that mate choice was unlikely to be particularly biased with respect to any trait. Another way to deal with this potential problem is to restrict the sample to individuals choosing from the same pool (Murphy 2008). Therefore we assessed assortative mating in the whole population as well as in just the newly formed pairs. By assessing only the newly formed pairs we also increased the chance that pairs had selected their mate based on their current morphology, as opposed to pairs that had been together longer. In newly formed pairs of this species we found no evidence for assortative pairing based on body size, condition and ornamentation.

It is certainly possible that assortative mating does occur in this species, either infrequently or in such a weak form as to be very difficult to detect reliably. Indeed, we did find some very weak support for assortative mating by wing length, body size and patch size, although none of these findings remained after correcting for the number of tests we ran, and none was found in more than a single year. In other species such as the blue tit *Cyanistes caeruleus* that have been more intensively studied, patterns of assortative mating have been reported in a single population in a single year (e.g. Andersson 1998), but have not been confirmed in other populations or across multiple years (e.g. Griffith *et al.* 2003). We believe that the different ways in which we have approached this question, and across multiple years, suggest that assortative mating is neither a consistent or strong phenomenon in this species with respect to the traits we have examined.

Interestingly, in other species in which assortative mating has been identified for a particular trait, that same trait is often found to relate to an important fitness related trait such as reproductive success (e.g. Masello & Quillfeldt 2003), or individual survival (e.g. Griffith *et al.* 2003). The traits for which we found weak indications of assortative mating (wing length, body size and patch size) may all conceivably be expected to relate to fitness, and have all

been found to be indicative of reproductive success in other passerine species. However, again, our analysis did not find clear indications of a role for any of these traits in predicting reproductive success.

Female ornament expression, body size or condition did not seem to affect the size of the clutch laid by female Long-tailed Finches, or the number of offspring fledged. This contrasts with previous findings in species such as the barn swallow *Hirundo rustica* in which female tail length reliably reflects female reproductive potential and the trait appears to be under directional sexual selection (Møller 1993). Our data is however consistent with previous studies of other species such as the House Finch *Carpodacus mexicanus* (Hill 1993), and blue tit (Parker *et al.* 2011) which also found no support for the idea that of the expression of colour in females was consistently related to quality. Higher ornamented males, larger males or males in better condition did not pair preferentially with females that laid larger clutches. The number of fledged offspring was slightly affected by male wing length and body size but not by male ornament expression. However ornamental traits do not have to be under direct selection each breeding season for them to be maintained by selection, they might only correlate with reproductive success during environmentally challenging years, or the focus of selection can change between years due to plasticity of female preferences (Chaine & Lyon 2008; Parker *et al.* 2011), or even spatially given different environmental contexts (Griffith *et al.* 1999; Parker *et al.* 2011). Whilst the rather obvious and extravagant throat patch, tail streamers and bill colour of the Long-tailed finch seem likely to have an ornamental function it is of course possible that they do not signal the quality of the bearer at all, and may therefore play no part in mate choice, but could signal e.g. parental quality (Hoelzer 1989; Griggio *et al.* 2010) or competitive ability (Griggio *et al.* 2010).

We found no evidence that ornament expression by males, and only very weak evidence that male size is predictive of reproductive output. However, in other socially monogamous species, male ornamentation has been shown to be a predictor of male fitness when gains and losses due to extra-pair fertilizations were taken into account (Albrecht *et al.* 2009), and that possibility remains to be investigated in this species.

If there is truly no assortative mating in this species, the most obvious explanation is that males and females in this species did not choose mates based on putative ornament expression, body size or body condition and the putative ornaments are not currently under sexual selection in this population. It is still not clear why females in mutually ornamented species express secondary sexual traits (reviewed by Amundsen 2000 and Clutton-Brock 2009). Very little support has been found for the sexual indistinguishability theory (Burley 1981), at all and was explicitly ruled unlikely for this species because the sexes can actually be reliably distinguished (Van Rooij & Griffith 2010). The possibility remains that only males gain sexually selected benefits from these ornaments, and that females express them due to genetic correlation (Lande 1980; Lande & Arnold 1985), or that females use them in other contexts (e.g. female competition over resources; Heinsohn *et al.* 2005; LeBas 2006). However, we have so far been unable to find any clear evidence for any form of direct selection on males or females, driven by independent or mutual sexual selection (e.g. Jones & Hunter 1993; Romero-Pujante *et al.* 2002; Kraaijeveld *et al.* 2004).

Our findings suggest that the expression of these apparently ornamental traits in both sexes of this species may play no current role in mutual mate selection, or as indicator traits of reproductive performance. We are currently unable to identify any function for these very elaborate putative ornaments in either sex of this species and suggest that the typical general assumption that all such traits have an ornamental function may need further examination (see

also Prum 2010). It is quite possible that putatively ornamental traits such as those investigated here are completely arbitrary characters that hold no information on the quality of the individual bearer other than the identification of an individual (Dale *et al.* 2001), the sex of the bearer or the species which they belong to, or that they had an important signalling role in the past which has now become redundant, leaving the traces of sexual selection in the past.

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CHAPTER SIX

The distribution of extra-pair paternity
is not related to ornamentation



In Preparation as: Erica P. van Rooij, E.P., Clare E. Holleley & Simon C. Griffith (). The incidence and distribution of extra-pair paternity is not related to the ornamentation of males or females in the long-tailed finch (*Poephila acuticauda*).

6.1 Abstract

Although the majority of passerine birds are socially monogamous, true genetic monogamy is rare, with extra-pair paternity (EPP) occurring in almost 90% of socially monogamous species. While males are normally assumed to engage in EPP to increase the number of offspring, in mutually ornamented species, males could potentially also increase the genetic quality of their extra-pair offspring by selecting a more attractive female. It has also been suggested that if females seek extra-pair paternity with males that are more attractive than their own partners this may increase the genetic quality of resulting offspring.

Here we report the occurrence of EPP in the socially monogamous long-tailed finch. With our array of microsatellite loci we were also able to identify a high proportion of extra-pair sires and compare them to the social males that were cuckolded. We also assessed the extra-pair male's mate choice by comparing his social female to the extra-pair females. We further investigated the possibility that extra-pair and within-pair offspring differed in quality during the nestling phase.

Extra-pair males sired 6.2% of offspring, which occurred in 17.9% of broods. We found no evidence that males select more attractive females to sire higher quality extra-pair offspring with. Females also did not select extra-pair mates that were more ornamented than their social mate and cuckolded males were not less ornamented than other males. The extra-pair offspring were not of higher quality than their half-siblings.

Our findings support a growing number of studies that have failed to find any obvious support for the good genes model of EPP in birds and we suggest that the adaptive benefits of EPP to females require further investigation.

6.2 Introduction

Most passerine birds are socially monogamous (Lack 1968), however true genetic monogamy is rare with extra-pair paternity (EPP) occurring in almost 90% of studied species (Griffith *et al.* 2002). There is a lot of interspecific variation in EPP, which follows deep-rooted phylogenetic variation in major life-history traits such as longevity, annual fecundity and patterns of parental care (Griffith *et al.* 2002). Within avian families that share broadly similar life-history and ecology there is still a lot of variation in the level of EPP. For example, within the Hirundines the level of EPP ranges from 14% in the fairy martin *Hirundo ariel* (Magrath & Elgar 1997) to 54% in the tree swallow *Tachycineta bicolor* (Dunn *et al.* 1994).

For females, engaging in EPCs does not increase the number of offspring produced by individual females like it does in males - females could even lose mate assistance or risk desertion if a female is caught by her mate (Dixon *et al.* 1994; Arnold & Owens 2002; Griffith 2007). In many species however females actively solicit or freely engage in EPCs (e.g. Smith 1988, Birkhead *et al.* 1990), which suggests that they benefit from them. As extra-pair males generally provide no resources to females, many studies have investigated the idea that females seek EPP with high quality males to gain some good genes benefits for at least some of their offspring (Birkhead & Møller 1992; Jennions & Petrie 2000). Females could base their choice of extra-pair males on the expression of male ornamental traits, which are often viewed as condition-dependent signals of male quality, to assess potential mates and thereby gain genetic benefits for their offspring (Andersson 1994; Cotton *et al.* 2004). More ornamented males often sire more extra-pair offspring (e.g. Møller & Birkhead 1994; Sheldon & Ellegren 1999; Thusius *et al.* 2001; Saino *et al.* 2007) and males with highest expression of ornamental plumage are more likely to father all offspring in their own broods (Saino *et al.* 1997; Sheldon & Ellegren 1999). However, in many other species extra-pair and within-pair

males were not different in terms of secondary sexual traits (e.g. Hill *et al.* 1994; Ratti *et al.* 1995; Krokene *et al.* 1998; Delhey *et al.* 2003; Akçay & Roughgarden 2007; Rosivall *et al.* 2009).

Males are normally assumed to engage in EPP to increase the number of offspring they sire. However, besides increasing the number of offspring, like females, males could also aim to increase the genetic quality of some of their offspring by copulating with a female more attractive than their social mate. In socially monogamous species with long-term pair bonds, males are as limited in choice of a partner as females and might therefore engage in EPC with high quality females to gain some good genes benefits for at least some of their offspring. Somewhat surprisingly, this perspective has not previously been examined, in part perhaps because it may be difficult to determine female quality in many species. However, in mutually ornamented species, males could actively select extra-pair females based on the expression of female ornamental traits, where female ornamentation may represent a condition-dependent signal of quality (e.g. Kraaijeveld *et al.* 2004b).

If males and/or females have EPCs to gain genetic benefits for extra-pair offspring this should result in better offspring growth, size or survival. A beneficial effect of extra-pair sires' genes has only been found in a few studies where extra-pair offspring and female's within-pair offspring were compared, on offspring condition (e.g. Sheldon *et al.* 1997), survival (Kempnaers *et al.* 1997), or enhanced offspring immunocompetence (Johnsen *et al.* 2000). In other studies however, extra-pair offspring did not grow faster or fledge larger (Krokene *et al.* 1998; Rosivall *et al.* 2009), or survive better (e.g. Lubjuhn *et al.* 1999). Besides predicted enhanced offspring quality, offspring sex could also be affected. As sons benefit more than daughters from inheriting their father's attractiveness traits (Trivers & Willard 1973; Charnov 1982), it should be adaptive for females to bias the sex ratio of extra-pair offspring in favour

of males (Sheldon & Ellegren 1996). Some studies have found biased allocation of sex with respect to extra-pair paternity (e.g. Johnson *et al.* 2009), but not others (e.g. Dietrich-Bischoff *et al.* 2006; Kraaijeveld *et al.* 2007).

If females engage in EPP only if they encounter a desirable extra-pair mate, breeding density might affect EPP rates as females will get to sample more males at high breeding densities (Birkhead & Møller 1992; Hill *et al.* 1994; Møller & Ninni 1998), but in many species no evidence for this idea has been found (e.g. Dunn *et al.* 1994; Sundberg & Dixon 1996; Westneat & Sherman 1997; Griffith *et al.* 2002). For the same reason EPP could be correlated to the distance to the nearest nest (Charmantier & Perret 2004), but not in all species (Dunn *et al.* 1994).

The mutually ornamented long-tailed finch is an endemic Australian estrildid finch. To date, the only other estrildid finch, for which paternity has been assessed is the zebra finch, which has a relatively low level of EPP for a finch, with between 1.7 - 2.4% of offspring being the result of EPP in 5 - 8% of broods in two different wild populations (Birkhead *et al.* 1990; Griffith *et al.* 2010). In this study we assess the level of EPP in a population of free-living long-tailed finches and investigate the occurrence of extra-pair paternity in relation with ecological and life-history factors. In this species we have previously shown variation in size of putative ornaments between males and females (Van Rooij & Griffith 2010). To assess whether siring extra-pair offspring is an important component of sexual selection in the long-tailed finch, we investigated whether morphological characters of males were linked with male success at defending the paternity of the chicks within his own nest and siring offspring in the nests of others and if this resulted in higher quality offspring. We also assessed, for the first time, whether males, besides increasing the number of offspring also increased the quality of their extra-pair offspring by selecting a more attractive female.

6.3 Methods

Study Species and Study Area

The long-tailed finch is a common Australian grass finch of the family Estrildidae, endemic to Northern Australia (Immelmann 1965; Higgins *et al.* 2006). Long-tailed finches are socially monogamous and pair bonds in this species are strong and last across multiple years with no evidence of divorce (Zann 1977; Van Rooij & Griffith 2011). Pairs are highly sedentary and remain in the same area during the breeding season and across years, with two or three nesting attempts per breeding season (Van Rooij & Griffith 2011). Both members of the pair participate in nest construction, incubation, brooding and feeding of the altricial young (Zann 1977; Higgins *et al.* 2006; Van Rooij & Griffith 2011).

Fieldwork was conducted during three breeding seasons (March to September) in three years (2008-10) near Wyndham, Western Australia (S15°33'38", E128°08'59"). The study area consisted of 108 ha of woodland savannah with Eucalypt trees providing natural cavities for nesting as well as artificial nest boxes supplied to facilitate this study (see Brazill-Boast *et al.* 2011).

Field Methods

We sampled 106 complete families (all offspring and both putative parents) over three breeding seasons (25 in 2008, 64 in 2009, 17 in 2010). All nest boxes were checked for new nesting attempts every six days. Active nests were checked daily from two days before the expected hatching date (12 days from the onset of incubation; Higgins *et al.* 2006). At the age of twelve days all nestlings were banded, and measured and a small blood sample was taken

(and stored in ethanol). All nests were checked just before fledging (age 16 days) and the nestlings present at that time were assumed to fledge.

Adults were captured and banded using mistnets at watering points (in creek beds) or with handnets on nests. Morphological measurements were taken of all adults, including patch size, tail streamer length, but for 80 adults only we also took measurements of colour with spectrometry (see Van Rooij & Griffith 2010 for methods). A small blood sample (<20µl) was taken from the brachial vein. All adults were banded with a numbered aluminium band (supplied by the Australian Bird and Bat Banding Scheme, ABBBS) and a unique combination of three colour bands. Putative parents were either captured while feeding the nestlings or parentage was confirmed by direct observation of colour-banded parents visiting the nest to feed the offspring.

Only in 2009, four measurements of each nestling were taken every other day from day 2 up until day 16: (1) body mass (g); (2) tarsus length (mm); (3) combined head and bill length (mm) (from the back of the head till the tip of the bill); (4) feather length of the 2nd tail feather (mm). All nestlings were measured between 6am and 10am. The measurements observed were obtained using digital callipers (0.01 mm) and with a digital scale (0.01g).

Age was categorized in the following way: ‘category 1’ - 1 year old - previous years nestlings; ‘category 2’ – adult at least 1 year old, when banded as adult of unknown age; ‘category 3’ - adult at least 2 years old, one year after being banded at unknown age; ‘category 4’ –adult at least 3 years old, 2 years after being banded at unknown age’. Pair bond duration was assessed as three categories: ‘old’ pairs had bred at least once before either in the same or previous season; ‘new’ pairs had not bred together before and were previously seen breeding

with another partner; ‘unknown’ pairs were not seen breeding before and pair bond duration could not be assessed.

Molecular Methods

DNA was extracted from blood samples using the PUREGENE DNA Purification Kit (Qiagen). We used five fluorescently labelled microsatellite loci (*Tgu1*, *Tgu3*, *Tgu4*, *Tgu8* and *Tgu12*) that had previously been isolated and characterised in the closely related zebra finch (Forstmeier *et al.* 2007). The molecular sex markers P2 and P8 were used to sex all adults and nestlings (Griffiths *et al.* 1998). All samples were run in two multiplex PCR reactions using a Qiagen Multiplex Kit at one-fifth the recommended volume. Samples were genotyped on a 48-Capillary 3730 DNA Analyser (Applied Biosystems, Foster City, CA, USA) using GS-500 (Liz) in each capillary as a size standard. Allele sizes were estimated on GeneMapper version 3.7 (Applied Biosystems 2004). Combined non-exclusion probabilities were calculated by CERVUS 3.0 (Kalinowski *et al.* 2007).

Identification of extra-pair sires was done with the parentage analysis module in CERVUS 3.0. Extra-pair offspring matched the extra-pair male at four loci (in 11 of 21 offspring) and 10 offspring matched the extra-pair male at all five loci and only one male matched the offspring at all loci (average LOD score 5.00 ± 2.21 (1.36 – 9.01)). For the 19 nests with 21 extra-pair nestlings in 16 cases an extra-pair sire was assigned. All putative mothers were found to be the genetic mothers of the offspring and confirm that no intra-specific brood parasitism occurred.

In the 112 adults genotyped, the loci were all highly variable with an average of 16 alleles per locus (range 10 – 19; Table 6.2). The combined non-exclusion probabilities calculated by CERVUS 3.0 for this set of markers in this population were $P = 0.012$ for the first parent and

$P = 0.001$ for the second parent. Most offspring and putative parents were successfully scored at all five ($n = 506$) microsatellite loci. Some were only scored at four loci, because one locus failed to amplify ($n = 25$; 4 were not scored for locus Tgu1; 6 for Tgu3; 11 for Tgu4; 2 for Tgu8; 2 for Tgu12).

Analysis

First we assessed the occurrence of EPP and intra-specific brood parasitism (IBP) in this species, by comparing offspring with both putative parents across five microsatellite loci. We then analyzed whether the occurrence of EPP in some nests was correlated to breeding density (nr of nests initiated 20 days earlier up to 10 days later than the focal nest in the same area) and distance to nearest occupied nest. We also tested whether the occurrence of EPP in certain nests was correlated to the duration of the pair bond.

All statistical tests were done in R Project for Statistical Computing (<http://www.r-project.org/>). The effect of ecological factors on the occurrence of EPP was tested in a generalized linear model (binomial distribution of EP nestlings per brood (0,1); with log link function) for 2009 data. We only used the 2009 data, as that season comprised the largest dataset and using only one season avoided pseudo-replication. Further, we tested whether extra-pair sires differed in secondary sexual characteristics (bill colour, patch size and tail streamer length), age and mass, tarsus and wing length from the within-pair males with paired samples t-tests and whether cuckolded males differed from non-cuckolded males for these same measures with ANOVAs.

To assess whether females selected extra-pair males based just on the fact they nested nearby, we mapped the nest location of the female's nest and the extra-pair male's nest, and all active

nests < 200m of the female's nest. We then compared extra-pair male morphology with the morphology of the males that nested < 200m of the female's nest with paired samples t-tests.

In 2009 only nestlings were measured every other day to assess growth rates, for 11 of the 12 broods that contained extra-pair offspring in this year (the twelfth was predated), nestling growth rates and size before fledging were measured. Effect of EPP on nestling growth rates and size before fledging were analyzed using Non-Linear Regression, following the analyses of Ricklefs (1967), using SPSS v17.0 statistical package. Growth parameters (A, K and t_i) were derived for individual nestlings by fitting logistic models of the formula:

$$W(t) = A / (1 + e^{-K(t - t_i)})$$

where $W(t)$ is the size of each character at time t , A is the asymptotic size, K is a measure of 'growth rate' and t_i the inflection point on the growth curve. Growth rate (K) and size before fledging was compared between extra-pair and within-pair offspring within the same brood, using paired samples t-tests.

Because twelve pairs bred in two different seasons and ten pairs bred twice in one season in the set of 106 nests, we tested for effects of pseudo-replication by comparing the incidence of extra-pair offspring across subsequent broods. We found no indication that individuals had a consistent tendency to have or not have extra-pair offspring in successive years (two-tailed Fisher's Exact test, all $p > 0.7$), and we therefore used each brood as independent data points (see also Reyer *et al.* 1997; Krokene *et al.* 1998).

Table 6.1. Incidence of extra-pair paternity (EPP) in a free-living long-tailed finch population near Wyndham, WA in 2008, 2009 and 2010.

Year	Number of broods	Number of broods with EPP	% broods with EP nestlings	Number of nestlings	Number of EP nestlings	% of EP nestlings
2008	25	5	20.0%	94	8	8.5 %
2009	64	12	18.8 %	258	15	5.8 %
2010	17	2	11.8 %	67	3	4.5 %
Total	106	19	17.9 %	419	26	6.2 %

6.4 Results

Extra-pair paternity in a wild population

We sampled 106 complete families over three breeding seasons (25 in 2008, 64 in 2009, 17 in 2010). Across the three years extra-pair males sired 4.5 - 8.5 % (mean 6.2 %) of all nestlings and 11.8 - 20.0 % (mean 17.9 %) of the broods contained one or two offspring sired by extra-pair males (Table 6.1).

Among the 419 nestlings (from 106 broods), 367 offspring matched with their putative parents at all loci with 52 offspring mismatching with one of their putative parents at one or more loci. As in each of these cases either the offspring or parent appeared to be a homozygote at that locus these mismatches could be explained by allelic dropout – the failure of an allele to amplify, and we therefore believe that these offspring are all the genetic offspring of their putative parents (5.3% in Tgu3, 5.7% Tgu4, 1.7% Tgu12 which were out of Hardy-Weinberg equilibrium; 0.5% Tgu1 and 1.2% Tgu8 which are in Hardy-Weinberg equilibrium)

The remaining 26 offspring (in 19 broods) all matched their putative mother at all loci but mismatched with the putative father at a minimum of three or more loci, and were the product of extra-pair sires. The average brood size in the families studied was 4.0 ± 1.0 , and most nests only contained one extra-pair offspring ($n = 12$), but some nests contained two extra-pair offspring ($n=7$).

Table 6.2. Allele size ranges, number of alleles, the level of heterozygosity, the probability of genotype sharing, Probability of false inclusion, Hardy-Weinberg equilibrium and null allele frequencies.

locus	Allele size range	Number of alleles found	Heterozygosity *	Probability of Genotype sharing [†]	Probability of false inclusion [‡]	HW	Null allele frequency estimate
Tgu1	170 - 192	10	90	1.9×10^{-2}	0.19	yes	0.0097
Tgu3	144 - 190	18	95	5.2×10^{-3}	0.10	no	0.0679
Tgu4	99 - 147	19	96	3.3×10^{-3}	0.08	no	0.2212
Tgu8	193 - 239	19	95	4.5×10^{-3}	0.09	yes	0.0417
Tgu12	101 - 139	16	94	7.7×10^{-3}	0.12	no	-0.0069
Combined				7.1×10^{-3}	0.12		

Based on the allele frequencies detected in 112 individuals (53 females, 59 males), which bred in the study area in 2008-2010.

* Heterozygosity was calculated as $(1-q)$, where q is the mean allele frequency derived from Cervus (following Sundberg & Dixon 1996).

[†] For a single locus the probability that two unrelated individuals will share the same genotype is given by $q^2(2-q)$ (Wong *et al.* 1987), where q is the mean allele frequency (following Sundberg & Dixon 1996).

[‡] For a single locus the probability of false paternal inclusion is given as $2q-q^2$ (Wong *et al.* 1987) (following Sundberg & Dixon 1996).

HW: Hardy-Weinberg Equilibrium; Null allele frequency estimate: calculated in Cervus

Ecological and life-history factors

For the 2009 dataset we analyzed the effect of ecological factors with a GLM, but none of the factors were significant: initiation date ($p=0.428$), breeding density ($p=0.856$) and distance to nearest active nest ($p=0.083$). Distance to nearest active nest was $84\text{m} \pm 48$ for nests that contained extra-pair offspring and $135\text{m} \pm 90$ for nests without EPP.

Neither female age nor male age affected the occurrence of EPP (female $F_{3,105} = 0.167$ $p = 0.919$; male $F_{3,105} = 0.370$ $p = 0.775$). Pair bond duration did not affect the occurrence of extra-pair offspring in a brood ($\chi^2 = 0.425$, $df = 2$, $p = 0.809$); of the ‘old’ pairs (that had bred together at least once before) 20 % had extra-pair offspring ($n = 35$), while 12.5 % of the ‘new’ pairs (one of whom was last recorded breeding with a different partner before) had extra-pair offspring ($n=16$). The pairs for which we were unable to determine the duration of their pair bond had a average level of EPP (18.2 % broods, $n=55$).

Several pairs had multiple broods within a single season (2 in 2008, 17 in 2009, 1 in 2010), of which ten pairs never had extra-pair offspring, while the other ten had extra-pair offspring in one brood but not in the other. Some pairs had multiple broods in different seasons; six of these never had extra-pair offspring in their broods while six others had extra-pair offspring in one brood but not in the other. One pair had EP chicks in 2 (of 5) broods in 2008 and 2009 (both times the first brood of the season). A consideration of the repeated reproductive events of these pairs revealed no consistent patterns with respect to the timing or incidence of EPP.

Table 6.3. Female morphology

Comparison of morphology between females whose mate engaged in EPP' and 'females whose mate did not engage in EPP' (with ANOVAs) and between social females and EP-females (paired samples t-test). Bonferroni correction $\alpha = 0.006$

Male	'females whose mate engaged in EPP' vs. 'females whose mate did not engage in EPP'			social female vs. EP-female		
	F	p	df	t	p	df
Age	5.359	0.023	105	-0.269	0.792	15
Pintail	0.412	0.522	101	-0.188	0.854	14
Patch size	8.663	0.005	58	-1.455	0.206	5
Bill colour	7.612	0.007	71	-0.221	0.831	8
Tarsus	4.085	0.046	96	-0.152	0.882	13
Wing	12.204	0.001	96	0.355	0.728	13
Mass	0.016	0.901	92	-0.418	0.683	13
Body size	0.003	0.956	96	-0.225	0.825	13

Table 6.4. Nestling growth parameters and fledge size.

	Female within-pair offspring vs. extra-pair offspring			Extra-pair male's offspring in own nest vs. extra-pair offspring		
	t	df	p	t	df	p
K tarsus	-0.260	10	0.799	0.738	7	0.485
K head-bill	-0.535	10	0.606	0.717	7	0.497
K mass	-0.944	10	0.367	-1.025	7	0.340
Fledge tarsus	-1.279	9	0.233	-0.855	6	0.426
Fledge head-bill	-0.169	9	0.869	0.308	6	0.768
Fledge mass	-1.152	9	0.279	0.105	6	0.920

Female quality

We found no difference in the morphology of ‘females whose mate engaged in EPP’ and ‘females whose mate did not engage in EPP’ for pintail, patch size, bill PC, tarsus, mass, body size or age, there was only a difference in wing length (Table 6.3). A pair-wise comparison of the social female and the extra-pair female showed that they did not differ in age, pintail length, patch size, or bill colour (Table 6.3). Neither did they differ in tarsus length, wing length, mass, or body size (Table 6.3).

To assess whether the extra-pair male improved offspring quality by having offspring with a female other than his mate we compared offspring quality (growth rate parameters and size at fledging) between his offspring and the extra-pair sired offspring. Growth rates did not differ between the offspring in his own nest and the extra-pair offspring, neither did size near fledging (Table 6.4).

Table 6.5. Male morphology.

Comparison of morphology between cuckolded and non-cuckolded males, between EP-males and the WP-males they cuckolded and between EP males and males nesting between the EP-males and the nest with EP-offspring.

Male	cuckolded males vs. non-cuckolded males ^{a,b}			WP-male vs. EP-male ^{a,c}			EP males vs. males nesting between the EP-males and the nest with EP-offspring ^{a,c}		
	F	p	df	t	p	df	t	p	df
Age	0.004	0.950	104	-1.000	0.333	15	1.594	0.155	7
Pintail	3.965	0.049	104	0.616	0.547	15	2.658	0.033	7
Patch	0.944	0.335	72	-1.518	0.159	10	0.274	0.793	6
size	0.216	0.644	77	-0.568	0.588	7	0.482	0.647	6
Bill	0.676	0.413	104	0.669	0.513	15	3.507	0.010	7
colour	0.000	0.992	104	-0.965	0.349	15	1.440	0.193	7
Tarsus	1.720	0.193	104	-1.725	0.105	15	1.350	0.219	7
Wing	1.010	0.317	104	0.130	0.898	15	2.955	0.021	7
Mass									
Body									
size									

a: Bonferroni correction $\alpha = 0.006$

b: ANOVA

c: Paired t-test

Male quality

Cuckolded males (18; one was cuckolded twice) lost one or two offspring per brood and paternity loss ranged from 20.0% - 66.7% ($35.7\% \pm 17.0$) of offspring per brood. Cuckolding males gained one or two extra offspring, which increased their success by 20 - 100% ($36.4\% \pm 22.8$). Four males both cuckolded and were cuckolded themselves, they together lost six offspring when being cuckolded and gained five offspring through cuckolding, three of the males gained the same number of offspring as they lost and the last male lost two offspring and gained only one. Males that were successful in gaining extra-pair offspring were not less likely to be cuckolded in their own nest ($\chi^2 = 0.603$, $df = 1$, $p = 0.437$).

We found no difference in the morphology of cuckolded males and males that were not cuckolded for pintail, patch size, bill PC, tarsus, mass, wing or body size, neither did they differ in age (Table 6.5). A pair-wise comparison of the within-pair male and the cuckolding extra-pair male showed that they did not differ in age, pintail length, patch size, or bill colour (Table 6.5). Neither did they differ in tarsus length, wing length, mass, or body size (Table 6.5).

To assess whether the female improved her offspring's quality by having extra-pair offspring we compared growth rate parameters and size at fledging for female within-pair offspring with extra-pair-offspring within the same brood. Growth rates did not differ between extra-pair and within-pair offspring, neither did size near fledging (Table 6.4). Sex ratio of extra-pair nestlings was not skewed towards males (EP: 7 of 26 females, 8 of 21 males; $\chi^2 = 0.667$, $df = 1$, $p = 0.414$).

Location of EP male

The location of the 16 nests with extra-pair offspring were mapped, together with the extra-pair male nest and all nearby active nests. Eight EP males nested in the same area at the time when the extra-pair offspring were fathered, 22 – 1593m ($489\text{m} \pm 492$) from the female's nest. These eight reproductively active extra-pair males' nests were at different stages at the time that the EPP was achieved. Four were building a nest, three were incubating their own clutch, and one was caring for the nestlings in his own social nest ($n=4$). Six EP males were not known to be nesting at the time they fathered the extra-pair offspring, but nested either earlier or later in the same season and also within the same kind of spatial range if we consider their breeding attempt that was closest to that in which they achieved EPP, ranging from 136-794m ($324\text{m} \pm 276$). The other two EP males were not recorded as nesting within the area during the same breeding season. Only one extra-pair male was the nearest neighbour to the female (6.3%).

Nests with extra-pair offspring had on average 1.5 ± 1.5 active nest within 100m, 3.8 ± 2.6 nests within 200m and 6.0 ± 2.8 nests within 400m. In only one case was the extra-pair male the closest nesting male. On average 4.6 ± 4.0 (ranging 0–11) males nested in between the female and the extra-pair male.

Extra-pair males did not differ in morphology from the males nesting between the EP-males and the nest of the EP-offspring (and $< 400\text{m}$ from the offspring's nest; $n = 8$) in age, pintail length, patch size, or bill colour (Table 6.5). Neither did they differ in tarsus length, wing length, mass, or body size (Table 6.5).

6.5 Discussion

Wild long-tailed finches breeding in the tropical savannah of northwest Australia had a relatively low level of EPP (6.2% offspring and 17.9% of broods), which is lower than the average level (11%) found across 100 species of socially monogamous birds (Griffith *et al.* 2002). The long-tailed finch is among the species with the lowest rates of EPP of the socially monogamous passerines (Griffith *et al.* 2002), with a slightly higher percentage than that found for the only other studied estrildid, the zebra finch, with 1.7-2.4% found in wild populations (Birkhead *et al.* 1990; Griffith *et al.* 2010). However, in the long-tailed finch, the percentage of extra-pair broods is much higher compared to 5-8% found in the zebra finch (Birkhead *et al.* 1990; Griffith *et al.* 2010).

We here assessed for the first time, whether males, besides increasing the number of offspring also increased the quality of their extra-pair offspring by selecting a more attractive female. We did not find evidence that the females with extra-pair offspring were of higher quality, as assessed by ornament expression, than other females in the population. Neither were extra-pair females more ornamented than the male's social mate. Some males did increase the number of offspring they sired, but the offspring were not of higher quality. Male variance in reproductive success is increased by EPP but the resulting offspring is not of higher quality.

Male ornamentation did not predict a male's success at defending the paternity of the nestlings within his own nest, even males successful at gaining EPP were not less likely to be cuckolded in their own nest. We did not find evidence that females select a higher quality extra-pair male than the male they are paired with and extra-pair offspring were not of higher quality than within-pair offspring, the same was found in another mutually ornamented species (black swan *Cygnus atratus* Kraaijeveld *et al.* 2004a). Females do not seem to choose

extra-pair males based on ‘good genes’ i.e. more ornamented males that sire better offspring, but might select males based on other factors, e.g. genetic compatibility. Alternatively, the putative ornaments in this species might not function as quality indicators and might not be important for mate selection of either social or extra-pair mates.

In monogamous species variation in reproductive success is generally less pronounced than in other species, suggesting more subtle ways in which sexual selection may work. Offspring sired through extra-pair copulations are one of several mechanisms that have been proposed to give rise to sexual selection in monogamous species (Kirkpatrick *et al.* 1990; Møller & Birkhead 1994). However only if males with a certain expression of ornamentation are more successful in siring extra-pair offspring than randomly selected males, then female choice of such males may be a major component of sexual selection in monogamous species (Birkhead & Møller 1992; Whittingham & Dunn 2005), especially in species like the long-tailed finch that form pair bonds that are maintained throughout the year and likely last for life (Zann 1977; Van Rooij & Griffith 2011).

Local breeding density did not affect the occurrence of EPP in broods, like in many other species (e.g. Dunn *et al.* 1994; Griffith *et al.* 2002), although if females engage in EPP only if they encounter a desirable extra-pair mate breeding density might affect EPP rates (Birkhead & Møller 1992; Hill *et al.* 1994; Møller & Ninni 1998). Floater males can also explain the absence of correlation between breeding density and EPP, as their presence is not accounted for in the estimation of breeding density (e.g. Leisler *et al.* 2000). In only one case (6.3%) was the extra-pair male the nearest neighbour, which was also found in other species (Sundberg & Dixon 1996; Charmantier & Perret 2004). The occurrence of extra-pair offspring was not related to breeding density or distance to nearest nest and identified extra-

pair males were not necessarily nearest neighbours, suggesting that extra-pair males are not chosen at random.

In summary, we found low rates of EPP in this species. Neither males nor females selected an extra-pair mate that was more attractive than their social partner. This suggests that their extra-pair offspring would be of no higher quality than their offspring with their social partner. The fact that extra-pair males are not usually nearest neighbours suggest they are not selected at random. Our findings therefore support a growing number of studies that have failed to find any obvious support for the good genes model of EPP in birds and we suggest that the adaptive benefits of EPP to females require further investigation.

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CHAPTER SEVEN

Synchronised provisioning at the nest:

high parental coordination



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high parental coordination in a monogamous species.

7.1 Abstract

Bi-parental care is very common in birds, occurring in over 90% of species, and is expected to evolve whenever the benefits of enhanced offspring survival exceed the costs to both parents of providing care. In altricial species, where the nestlings are entirely dependent on the parents for providing food until fledging, reproductive success is related to the capacity of the parents to provision the offspring at the nest and often for some weeks after fledging. The degree to which parents synchronise their visits to the nest is rarely considered by studies of bi-parental care, and yet may also affect the outcome of the reproductive attempt, and the dynamics of sexual conflict between the parents.

We studied parental care in the long-tailed finch (*Poephila acuticauda*), a socially monogamous species with bi-parental care. We monitored parental nest visit rates and the degree of parental visit synchrony, and assessed their effects on breeding success (e.g. brood size, number of offspring fledged and nestling growth).

Nest visit rate was very low in this species (< 1 visit/h), but increased with larger brood sizes. The nest visit rates of partners were strongly correlated, largely due to the high degree of visit synchrony, with pairs visiting the nest together on at least 83% of occasions. Our data suggest that the natural variation in the degree of pair synchrony has a very limited effect on the number of fledglings produced in a breeding attempt. The high degree of parental synchrony at the nest may reflect the ‘togetherness’ of the couple but does not reflect the duration of the pair bond. Our findings suggest that nest visit synchrony may either relate to the benefit of parents being together whilst foraging away from the nest, or may reduce nest predation by halving the number of bursts of nestling begging and activity around the nest during feeding visits.

7.2 Introduction

Parental care is common in birds, with bi-parental care occurring in more than 90% of species (Clutton-Brock 1991), and is expected to evolve whenever the benefits of enhanced offspring survival exceed the costs to both parents of providing care (Clutton-Brock 1991). In altricial species, where the nestlings are entirely dependent on the parents for providing food until fledging, reproductive success is often limited by parental feeding rates (e.g. Royle *et al.* 2006). However, provisioning involves energy expenditure by the parents, which may have a negative effect on their future reproduction through trade-offs with survival (e.g. Nur 1988) or attractiveness (e.g. Griffith 2000). Since each parent's own future potential would be enhanced if the other parent contributed more of the total investment in offspring, there is an interesting conflict between the sexes (e.g. Trivers 1972; Royle *et al.* 2002; McNamara *et al.* 2003).

Nest visit rate differs between the sexes in some avian species, with females provisioning at a greater rate in some species (e.g. Markman *et al.* 1995; Sanz & Tinbergen 1999; Bulit *et al.* 2008), while in other species feeding rates are more equitable between males and females (e.g. Tremont & Ford 2000; Royle *et al.* 2006; Lee *et al.* 2010).

Typically food delivery rates are expected to be positively related to brood size as more offspring require more food (e.g. the positive correlation found across 44 species of bird Martin *et al.* 2000). However, in some species, parental visit rates are unaffected by brood size and subsequently in larger broods, individual chicks receive less food (e.g. Emms & Verbeek 1991). Studies that have used experimental brood size manipulations, have typically found that the observed relationship between visit rate and brood size is driven by nestling need, with enlarged broods receiving an increased rate of visits by both or at least one parent (e.g. Markman *et al.* 1995; Moreno *et al.* 1995; Sanz 1997). The optimal growth rate of

nestlings is partly determined by the ability of the parents to supply energy to the growing nestling (e.g. Naef-Daenzer & Keller 1999; Huin *et al.* 2000).

However, as well as being driven by the needs of the offspring and the life-history of the individual parents, a number of other factors are believed to play an important role in determining the frequency of nest visits by the parents. For example, local breeding density may have a positive effect on feeding rates possibly due to benefits of foraging with conspecifics (Lee *et al.* 2010), but other studies have revealed the opposite pattern (Sillett *et al.* 2004). Also, the chance that predators will detect a nest increases with parent visit rate (Skutch 1949; Martin *et al.* 2000; Muchai & DuPlessis 2005), causing birds to adjust their nest visit rate to the local predation risk (Eggers *et al.* 2005; Fontaine & Martin 2006). Visit rates also vary dramatically according to the feeding ecology of species. For example carnivorous raptors deliver large food items at a very low frequency (e.g. Dykstra *et al.* 2003), while others including insectivorous birds deliver small items very frequently (Lee *et al.* 2010; Michler *et al.* 2010) and species that feed their nestlings with seeds have intermediate delivery rates (e.g. Krebs *et al.* 1999; Budden & Beisinger 2009; Gilby *et al.* 2011).

Over the past couple of decades, possibly because of the interest in sexual conflict suggested by Triver's (1972) classic paper, much of the research into bi-parental care has investigated the sources of variation in the level of care provided by individual males and females, particularly in the context of theoretical ideas such as the good-parent hypothesis (Hoelzer 1989), and the differential allocation hypothesis (Burley 1986). These hypotheses and much of the work that has followed (e.g. Royle *et al.* 2002) has focused on the different investment strategies of males and females and the potential conflict between the sexes. By contrast, rather less work has focused on the strategies that socially monogamous parents use to coordinate the care that they provide to their offspring. Synchronized behaviour by the two

parents will tend to arise when the benefit of synchrony outweighs the costs associated with either delaying or bringing forward a change in behaviour (Lima 1994; Dostalkova & Spinka 2007), and might be advantageous where individuals cooperate to achieve a common goal, like feeding nestlings (Spoon *et al.* 2006). In order to synchronize activities an individual may have to compromise its own activity budget, which will entail a cost (e.g. Conradt & Roper 2000). Synchronized feeding visits by helpers-at-the-nest have been observed in several cooperatively breeding avian species (e.g. Doutrelant & Covas 2007; McDonald *et al.* 2008; Raihani *et al.* 2010), and in a highly social flock-living parrotbill (Lee *et al.* 2010). Here we present one of the first detailed investigations of parental synchrony in a typical socially monogamous passerine – the long-tailed finch *Poephila acuticauda*.

The long-tailed finch is an endemic Australian grassfinch which is ecologically very similar to the zebra finch (Van Rooij & Griffith 2011) although it inhabits the tropical savannah in the north of Australia, rather than the more arid open country that is home to the zebra finch. Long-tailed finches are primarily granivorous, but supplement their diet with small invertebrates (Higgins *et al.* 2006), particularly during breeding. They are socially monogamous and pair bonds in this species are very strong and durable (Zann 1977; Van Rooij & Griffith 2011). They preferentially nest in cavities and breed readily in artificial nest-boxes (Van Rooij & Griffith 2011). Nest building, egg incubation and nestling provisioning is conducted jointly by the pair (Higgins *et al.* 2006; Van Rooij & Griffith 2011). We here describe parental nest visit rates and visit synchrony in a wild population of long-tailed finches and examine potential effects on breeding success, nestling development and condition. We also investigated the extent to which visit rate and synchrony were predicted by social factors such as breeding density and the duration of the pair bond.

7.3 Methods

Study Area and Species

During the breeding season of 2009 (early March till late September), data was collected on long-tailed finches breeding near Wyndham, in northwest Australia (S15°33'38", E128°08'59"). All of the pairs in this study nested in boxes that were erected to facilitate the study of both Gouldian finch (*Erythrura gouldiae*) and long-tailed finches in this area (see Brazill-Boast *et al.* 2011; Van Rooij & Griffith 2011). Adult long-tailed finches are only slightly dimorphic and therefore all sexes were confirmed with molecular sex markers (Griffiths *et al.* 1998). Long-tailed finches can raise several broods per season, with brood sizes varying from two to seven (4.3 ± 1.0 ; Van Rooij & Griffith 2011) and nestling period (20.6 ± 2 days).

Fifty five banded pairs were studied breeding in the area in 2009, 28 pairs had only one recorded breeding attempt (51%), 14 pairs had two recorded breeding attempts (25%) and 13 pairs had three breeding attempts (24%). At the age of ten days all nestlings were banded, measured and weighed and a small blood sample was taken. Nestlings were weighed every other day from day two till day 16.

Breeding density was calculated as the number of active nests initiated from 20 days earlier than the initiation date of the focal nest till up to 20 days later. These nests will still be active when the focal nest hatches; average length of breeding attempt is 39 days minus egg laying time (5 days) and incubation time (14 days). Pairs starting within this period were still active while the focal was raising nestlings) than the focal nest in the same area. 'Distance to nearest nest' was calculated as distance to nearest occupied nest initiated during the same period.

In monitored nesting attempts we counted eggs and inspected nests daily at the predicted time of hatching. The number of hatchlings was counted and nestlings were subsequently monitored until they fledged. Nestling measures of day 16 were used as a measure of offspring quality, and we assessed the size difference (in mass) between nestlings as a percentage difference between smallest and largest offspring, to determine the extent to which parents produced a brood of even quality. We also computed a body condition index as the residuals from a linear regression of body mass on tarsus length as is commonly used (Ots *et al.* 1998) and calculated the difference in condition between the best and the poorest nestling.

Pair duration was categorized in three ways: (a) whether the pair bred together before (0 is never bred together before; 1 is bred together at least once before), (b) the number of seasons a pair bred together (0, 1, 2; including the current season if the pair bred together earlier in the current season) and (c) the number of times the pair bred together over the seasons (range 0 to 4).

A number of morphological traits were assessed for each parent. Tarsus, bill, tail and pintail length (to the nearest 0.1mm), wing length (to the nearest 0.5mm) and body mass (to the nearest 0.1 g) were measured. Patch size was measured from photos of each individual taken in a standardised posture, restrained in an artificial holder with the head tilted back (for detailed methods see Van Rooij & Griffith 2010). Spectral reflectance of the upper mandible was measured in three consecutive scans taken from the centre of the bill (for detailed methods see Van Rooij & Griffith 2010). Bill colour was summarized into one Principal Component (PC1; explaining 94% of variation in this population). Age was categorized in the following way: ‘category 1’ - 1 year old - previous years nestlings; ‘category 2’ – adult at least 1 year old, when banded as adult of unknown age; ‘category 3’ - adult at least 2 years old, one

year after being banded at unknown age'; 'category 4' –adult at least 3 years old, 2 years after being banded at unknown age'.

Catching and Molecular Sexing

Long-tailed finches were caught with handnets on their nests or in mistnets at creeks and water holes near nesting sites. All adult birds were banded with an individually numbered metal band (ABBBS) and individual colour combinations. In successful broods, when nestlings were 12 days old, they were banded with a metal band and a small blood sample was taken from the brachial (wing) vein of adult birds and 12-day-old nestlings to facilitate molecular sexing. All individuals were sexed using the molecular sex markers P2 and P8 (Griffiths *et al.* 1998). The reliability of the sexing was confirmed by the observation that the two adults caught on an active nest, were always one female and one male ($n = 55$).

Parental nest visit rates

To assess the rate of parental feeding visits we used video cameras (AVC 647 Color IR Camera; 1-2m from the entrance of the nest box and connected to a harddrive Archos 605 WIFI), which filmed the entrance of the nestbox. Birds were acclimatized to the camera over a minimum 24-h period prior to recording. A total of 50 nesting attempts were filmed from 42 independent pairs. However, seven nests were removed from subsequent analysis because one parent did not feed nestlings during the period of filming, but were directly observed (using binoculars) feeding the nestlings once the camera was removed. Individual parental identity was scored from the films by E.P. van Rooij. To allow easy individual recognition of the parents when entering the nest, one of the parents was marked with a white dot on the back of the head (tipp-ex). This mark was made during capture between six and two days before

filming and although the mark did wear off eventually it was usually quite clear on the films over this timeframe. For eight pairs we could not differentiate between the two individuals as they visited the nest because either we had been unable to catch and mark them or, the mark had worn off. These eight pairs were also excluded from subsequent analyses. Eight of the filmed nests were second or third broods of pairs that had been filmed rearing their first brood. The sample size for the analysis of feeding rates to first broods was therefore 29 pairs, with an additional six pairs filmed feeding second broods, and two pairs feeding third broods. These 29 independent pairs were used for all analyses. The six second broods and two third broods were used in only one analysis which compared later broods to the first brood.

Nests were filmed when nestlings were ten and eleven days old, coinciding with the period of maximal nestling growth (Van Rooij pers. observations). Recording started around 6am (just after sunrise) and continued for around 10 hours per day (total 367 hours filmed; 9.9 hours (594 min. \pm 74 min) per day). The videos were analysed using VLC media player.

The number of visits to the nest by each parent was recorded, and the nest visit rate by the pair was assessed (overall nest visit rate: 'total number of individual visits of both pair members combined' per 'number of hours filmed'). We also calculated nest visit rate separately for females (female nest visit rate: 'number of visits to the nest by the female' per 'number of hours filmed') and males (male nest visit rate: 'number of visits to the nest by the male' per 'number of hours filmed'). Time spent inside the nestbox was also assessed.

The effects of nest visit rates and nest visit synchrony on breeding success (brood size, number offspring fledging) were analyzed with correlations, paired t-tests and General Linear Models. The relationship between nest visit rate and nest visit synchrony with male and female morphology was assessed with correlations.

Nest visit synchrony

We considered that males and females were together at the nest (i.e. a synchronous visit) if they arrived at the tree together and the second individual to enter the nest box entered the nest box within 5 minutes of the time that the first individual entered the box. We then calculated the proportion of visit together as: (number of visits together x 2) / total number of visits by individuals. If the second individual entered the nest box more than 5 minutes after the first individual we considered them to have visited separately (further justification of this becomes apparent in the results section).

We calculated the time each parent was present at the nest the following way: ((5 min transition time + mean visit duration) x mean individual daily visit rate / mean time filmed) x 100). A transition time of 5 min was added for the bird to wait in the tree before going into the box. On average, each parent was present at the nest for an estimated $((5+1.65) \times 7.72 / 594) \times 100 = 8.6\%$ of the day. If male and female visited the nest independently of each other and randomly, we would expect them to be recorded at the nest together $8.6 \times 8.6\% = 0.74\%$ of the time. We calculated expected time spent at the nest together for each pair separately and compared them with observed proportion of time spent at the nest together with paired t-tests.

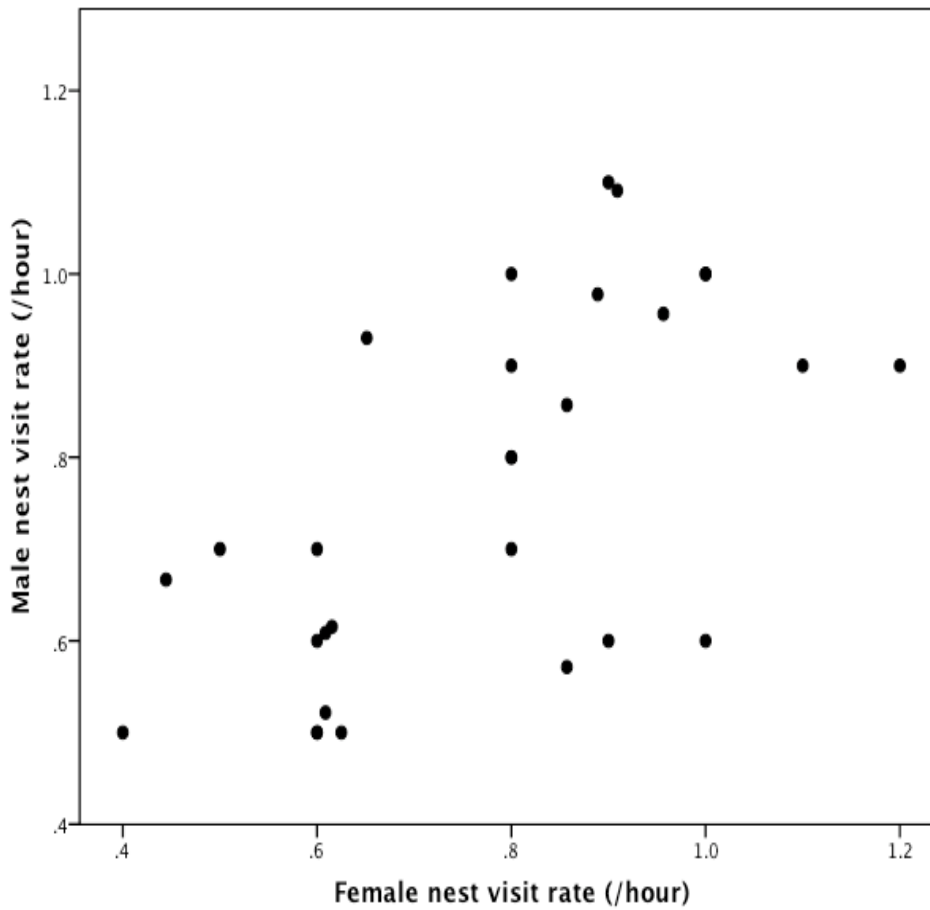


Figure 7.1 Nest visit rate (visits/hour) by males and females.

There was a positive correlation between the individual female nest visit rate and male nest visit rate at all nests ($r_s = 0.611$, $p < 0.001$, $n = 29$).

7.4 Results

Parental provisioning

Long-tailed finches cared for their young by feeding them as a pair, arriving at the nest together (83% of the nest visits) and entering the nestbox individually and sequentially to feed the nestlings. Nest visit frequency was quite stable over the day with, on average 0.77 (± 0.10) individual visits per hour. However, the visit rate was lowest in the middle of the day: individual nest visit rate was 0.66 visits per hour between 10-11am and 2-3pm; and highest in the first hours after sunrise: 0.97 visits per hour between 6 – 8am; average sunrise was at 5.45am).

On average 3m24s ($\pm 8m36s$) was spent in the nestbox during an individual visit. This high variation was caused by some occasional visits in excess of over 10 min (28 of 435 visits; 17 of these visits were by females and 11 by males of which 5 visits were by one particular male and were spread throughout the day; all visits under 10 minutes were far below the 10 minute mark). It is not clear what the parent was doing in the nest box during these extended visits as the ambient temperature ranged between 20.6 and 34.9 degrees (Bureau of Meteorology), and the nestlings were all at least ten days old and would not have required brooding. When removing these exceptional 28 visits the mean time spent inside the nestbox per visit was 1m39s \pm 1m19s. Males spent 1m46s \pm 50s per visit and females 1m41s \pm 56s.

Nest visit rate

There was a positive correlation between the individual female nest visit rate and male nest visit rate at all nests (Spearman correlation: $r_s = 0.611$, $p < 0.001$, $n = 29$; Figure 7.1), and at

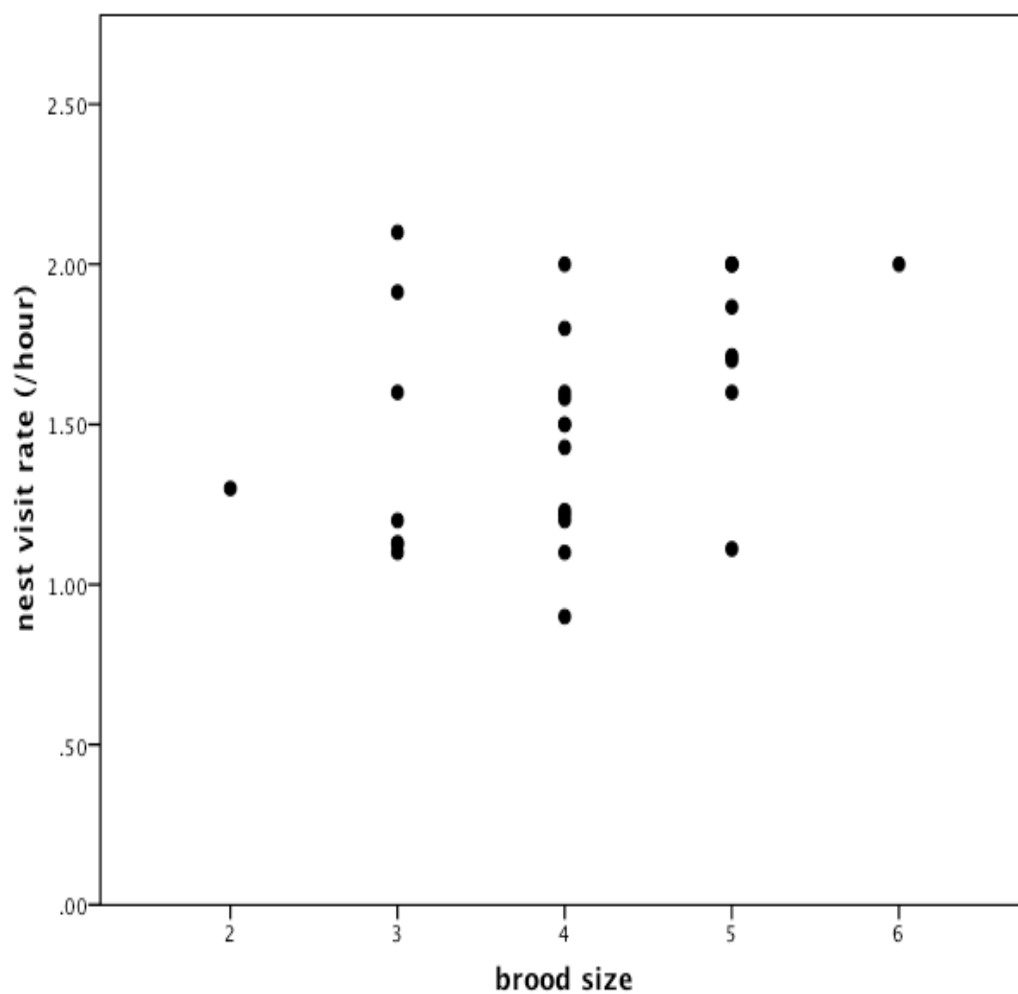


Figure 7.2a Brood size vs nest visit rate.

Brood size vs nest visit rate. Overall nest visit rate was affected by brood size (GLM $F=2.135$, $p=0.044$; Table 7.1).

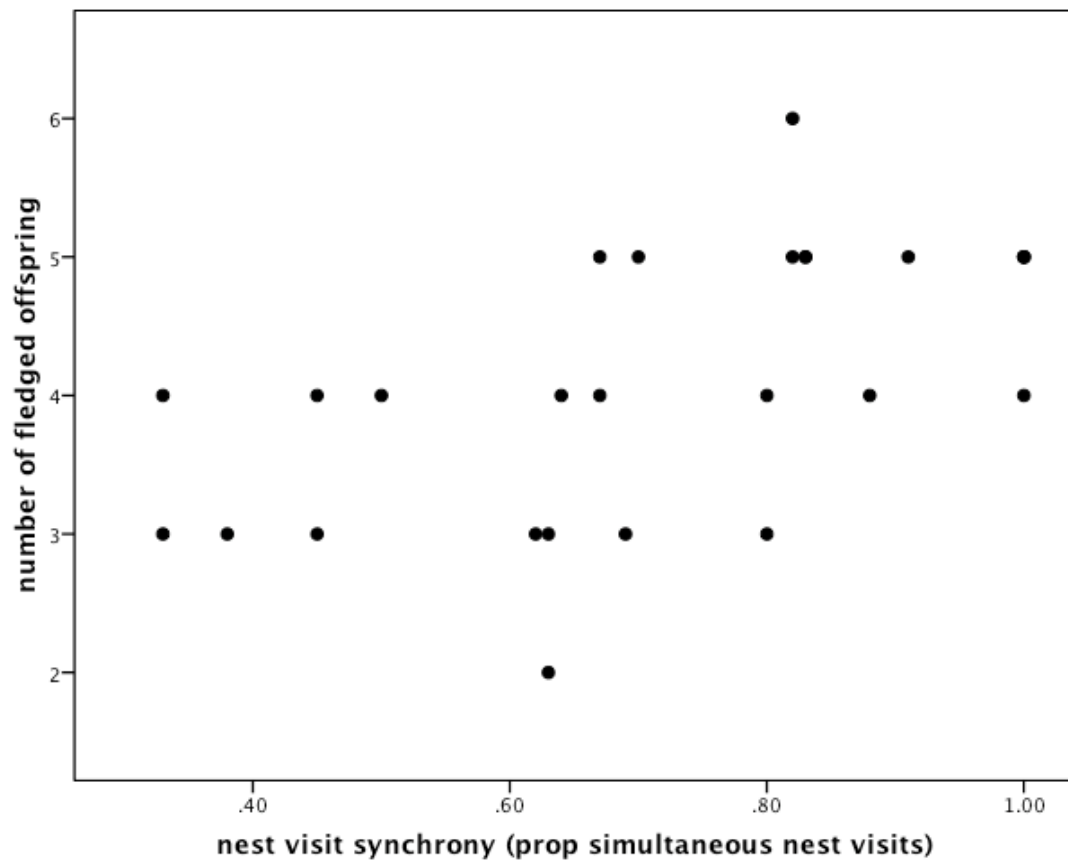


Figure 7.2b number of fledglings vs. synchrony.

Number of fledglings vs. nest visit synchrony. There was a tendency for nest visit synchrony to affect the number of offspring fledged (GLM $F=1.888$, $p=0.071$; Table 7.1).

Table 7.1 Overall nest visit rate and nest visit synchrony in relation to breeding success and environmental factors.

	GLM	overall nest visit rate	nest visit synchrony
brood size	F	2.109	-0.902
	p	0.046 *	0.376
nest succesfull	F	1.000	-1.869
	p	0.327	0.074
number fledging	F	-1.153	1.888
	p	0.261	0.071
hatch success	F	-1.795	1.413
	p	0.085	0.171
% difference nestling mass	F	0.061	0.352
	p	0.952	0.728
difference condition	F	0.373	-0.267
	p	0.713	0.792
nesting density	F	0.756	0.328
	p	0.457	0.746
initiation day	F	0.208	0.121
	p	0.837	0.905

*. Correlation is significant at the 0.05 level (2-tailed). n=29

each nest there was no difference between male and female nest visit rate (Paired-samples t-test $t_{28} = 0.351$, $p = 0.728$).

Overall nest visit rate (total number of individual visits of the pair combined per number of hours filmed) was related to brood size (GLM $F=2.135$, $p=0.044$; Figure 7.2a). Overall nest visit rate did not affect whether the nest was successful (fledged all offspring), nor did it affect the number of offspring a pair fledged (Table 7.1). Overall nest visit rate was slightly related to hatching success (GLM $F=-1.795$, $p=0.085$; Table 7.1).

Overall nest visit rate did not affect difference in brood condition, difference in mass (Table 7.1) among nestlings within broods. Overall nest visit rate was not affected by nesting density or initiation date (Table 7.1).

Male size (mass, tarsus) and ornamentation (pintail, patch size, bill colour) were not correlated to male nest visit rate (Table 7.2) and female size (mass, tarsus) and ornamentation (pintail, patch size, bill colour) were not correlated to female nest visit rate (Table 7.2). Male nest visit rate was not affected by male age ($F_{3,28}=1.593$, $p=0.216$) and female nest visit rate was not affected by female age ($F_{2,28}=0.534$, $p=0.592$).

Table 7.2 Adult morphology.

Female nest visit rate vs. female morphology, male nest visit rate vs. male morphology compared with Spearman correlations. Nest visit synchrony was compared to female and male morphology with Spearman correlations. Bonferroni correction for five comparisons lowers α to 0.01.

		Female nest visit rate vs. female morphology	Male nest visit rate vs. male morphology	nest visit synchrony vs. female morphology	vs. male morphology
Mass	rs	0.014	0.225	-0.434	-0.075
	p	0.947	0.250	0.024	0.706
	n	27	28	27	28
Tarsus	rs	-0.215	-0.052	-0.177	-0.159
	p	0.281	0.795	0.377	0.419
	n	27	28	27	28
Pintail	rs	0.022	-0.197	-0.066	-0.140
	p	0.913	0.316	0.743	0.476
	n	27	28	27	28
Patch size	rs	-0.270	-0.289	0.123	-0.420
	p	0.312	0.193	0.650	0.052
	n	16	22	16	22
Bill colour	rs	-0.382	0.128	-0.003	-0.323
	p	0.106	0.551	0.991	0.124
	n	19	24	19	24

Nest visit synchrony

Nest visit rate was very low in this species. Parents usually arrived together and tended to perch in the nesting tree together before the first bird entered the nest. The second bird usually waits outside the nest while the first one is in there, and then when the first bird exits the nest it remains in the nest tree while the second bird enters the nest. Partners visited the nest together on average during 82.7% (± 14.9) of nest visits, which is significantly more than expected by chance (observed proportion of synchronous nest visits vs. the time together at the nestbox when assuming random nest visit behaviour; paired t-test $t = -19.071$, $p < 0.001$, $n = 29$). Nest visit synchrony was independent of overall nest visit rate ($r_s = 0.204$, $p = 0.288$, $n = 29$). Five pairs always visited the nest together (17% of pairs), with, on average, 8 synchronous visits per pair. In the other 24 pairs the average proportion of synchronous visits was 79% with the minimum number of synchronous visits by any pair being 3 out of 6 by each individual.

There was a tendency for nest visit synchrony to affect the number of offspring fledged (GLM $F=1.888$, $p= 0.071$; Figure 7.2b) and whether a nest was successful in fledging any offspring or not (GLM $F= -1.869$, $p= 0.074$). Nest visit synchrony did not affect brood size (Table 7.1). Nest visit synchrony was not related to hatching success (Table 7.1); did not affect difference in mass or difference in condition (Table 7.1) among nestlings within broods; and was not affected by nesting density or initiation day (Table 7.1).

Male size (mass, tarsus) and ornamentation (pintail, patch size, bill colour) were not correlated to nest visit synchrony (Table 7.2) and female size (mass, tarsus) and ornamentation (pintail, patch size, bill colour) were not correlated to nest visit synchrony (Table 7.2). Nest visit synchrony was not affected by male age ($F_{3,28}=0.253$, $p=0.859$) or female age ($F_{2,28}=2.049$, $p=0.149$).

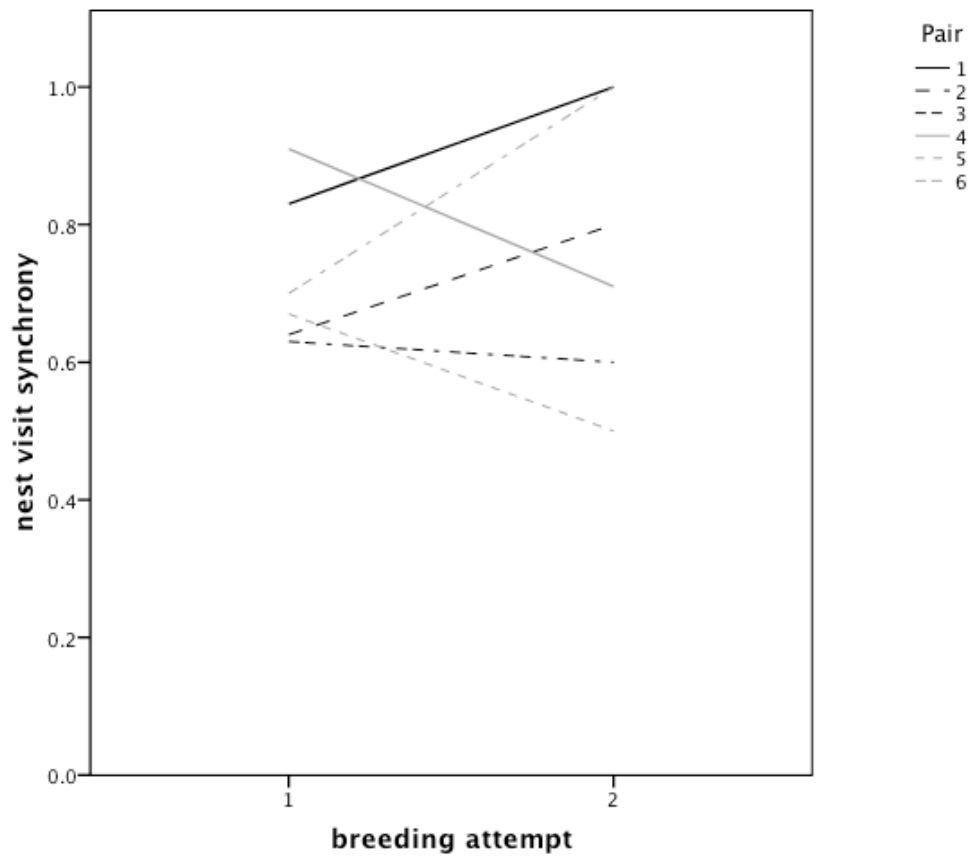


Figure 7.3 Nest visit synchrony in first, second and third broods per pair.

Data for the six pairs for which we recorded multiple breeding attempts. Black lines indicate those pairs that had never bred together before (pair 1-3), grey lines indicate those pairs that had bred together before (pair 4-6).

Effect of pair bond on nest visit rate and synchrony

Overall nest visit rate and nest visit synchrony were not affected by pair bond duration, i.e. whether a pair bred together before or not (nest visit rate $F_{14,16}=1.034$, $p=0.596$; synchrony $F_{11,16}=1.417$, $p=0.396$), the number of seasons the pair bred together before (nest visit rate $F_{19,28}=0.661$, $p=0.787$; synchrony $F_{15,28}=1.462$, $p=0.249$) and the number of times the pair bred together over the seasons (nest visit rate $F_{4,28}=0.770$, $p=0.556$; synchrony $F_{4,28}=1.573$, $p=0.214$).

A small number of pairs were followed during two ($n=6$), or three nesting attempts ($n=2$). Overall nest visit rate only slightly differed between first, second and third broods ($F_{2,13} = 3.163$, $p=0.082$) and overall there was no increase in synchrony between the first and the second recorded breeding attempt (Paired t-test $t_5 = -0.463$, $p = 0.663$; Figure 7.3). Three of these pairs had bred together before and did not differ in synchrony between the first and second recorded brood (Paired t-test $t_2 = 0.144$, $p = 0.899$), the other three pairs had never been recorded as breeding together before but did not show increased synchrony between the first and second brood (Paired t-test $t_2 = -1.537$, $p = 0.264$). For both pairs that bred three times together, the third time the nest visit synchrony was not different from the first (Paired t-test $t_1 = 0.909$, $p = 0.530$) and second (Paired t-test $t_1 = 1.320$, $p = 0.413$) breeding attempt.

7.5 Discussion

In this study of parental care in the long-tailed finch, we found that nest visits are very infrequent – each partner visited the nest on average less than once an hour – but highly synchronised between the male and female. Parents at the same nest provisioned their nestlings at similar rates, and nest visits were synchronized between pair members in 83% of all nest visits. More synchronous pairs may have produced more fledglings, though this was only marginally significant. Otherwise there was no evidence that synchrony affected breeding success.

The effect of parental feeding rates at the nest has been the focus of many studies, but not many species exhibit nest visit synchrony and few studies have considered why synchrony in parental feeding visits might occur. Nest visit synchrony is high in this species, and comparable to the ecologically similar zebra finch (Gilby *et al.* 2011). We did find some very limited evidence that synchronized nest visits may affect the reproductive success in this species. Nest visit synchrony however can be linked to foraging synchrony as individuals often forage with their breeding partner or members of the breeding group (e.g. Zann 1996), therefore nest visit synchrony in this species could simply have developed as a side effect of the pair feeding together. Synchronization might be easier for granivorous species like the long-tailed finch because the food source does not move and is more predictable, compared to species that feed their young e.g. invertebrates which are more difficult to capture and locate, and therefore may not be able to synchronize nest visits. This might also explain why in this species with very strong pair bonds not all nest visits are synchronized, as insects are used to supplement the diet, which might make individual nest visits necessary. Nest visit synchrony has also been suggested to play a role in minimization of nest disturbance and reducing predator attraction (Raihani *et al.* 2010), especially in species like the long-tailed finch where

the nest cavity is concealed and predators in the nest are not visible from the exterior (e.g. Doutrelant & Covas 2007). In this population breeding in nest boxes predation rates were relatively low, therefore it is highly possible that predation and halving the amount of activity around the nest is a primary selective force behind synchrony. Pairs forage together and also visit the nest together (and enter one at a time) so they can very effectively look out for one another and essentially be a sentinel for each other. Synchrony has also shown to be affected by breeding density and the proximity of neighbours (Lee *et al.* 2010) but we found no similar effects here.

Nest visit synchrony did not seem to increase with pair bond duration, although it has been suggested that increased pair duration may allow increased familiarity between mates and therefore better coordination of parental care (Fowler 1995; Black 1996). We expected an increase in synchrony in pairs that had been together for longer, as this is a life-mated species (Zann 1977), but we found no increase in synchrony in consecutive broods for pairs that had bred together before the focal nesting attempt over pairs that had not bred together before. However, for the pairs we had not seen breeding together before we don't actually know how long they had been together. Long-tailed finches are a sedentary species and the pair may have actually been socially bonded for many months before the first attempt, which is sufficient time to have become very synchronized. The high degree of parental synchrony at the nest therefore may reflect the 'togetherness' of the couple but does not reflect the duration of the pair bond. This 'togetherness' may also be affected by the similarity of parental personalities which in turn may have a positive effect on reproductive success (Schuett *et al.* 2011) as well vocalizations between pair members (Elie *et al.* 2010).

Nest visit rate was very low in this species, with similarly low nest visit rates found in other granivorous species (e.g. crimson rosella *Platycerus elegans* Krebs *et al.* 1999; green-rumped

parrotlet *Forpus passerinus* Budden & Beisinger 2009). Males and females provisioned the nestlings at similar rates, which is also found in several other species (e.g. leaden flycatcher *Myiagra rubecula* Tremont & Ford 2000; zebra finch *Taeniopygia guttata* Royle *et al.* 2006; vinous-throated Parrotbill *Paradoxornis webbianus* Lee *et al.* 2010). Although we found the nest visit rate to be relatively low, it did increase with larger brood sizes, but did not affect any other measure of breeding success assessed here. In this species however it is unknown whether nest visit rate is an accurate measure of food delivered to the nestlings, which in some species is correlated (e.g. house finches *Carpodacus mexicanus* Nolan *et al.* 2001; tree swallows *Tachycineta bicolor* McCarty 2002), but not in others (e.g. zebra finch Gilby *et al.* 2011). Although found in a variety of species (Naef-Daenzer & Keller 1999; Lee *et al.* 2010), we did not find a significant relationship between parental nest visit rate and nestling growth, presumably because parents adjusted nest visit rate with brood size and nestlings in larger broods did not receive more food than those in smaller broods fed at lower rates. None of the ecological factors considered (e.g. breeding density) seemed to affect nest visit rate.

Parental morphology has been predicted to affect variation in the quality of parental care effort (Hoelzer 1989), however in our study neither male nor female morphology affected nest visit rates or synchrony. Neither did we find evidence that more attractive adults provided less parental care because mates are willing to increase their contributions to keep their partners (Burley 1986), which has been found in some other passerines (e.g. Duckworth *et al.* 2003; Limbourg *et al.* 2004). In some other species, pairs that mate assortatively often do better (e.g. Black *et al.* 1996), but in long-tailed finches no evidence has been found for assortative mating or higher reproductive success in more ornamented individuals (Van Rooij and Griffith *subm.*).

We found that nest visit rate was very low in this species but that nest visits were highly synchronous. We suggest that the high degree of parental synchrony at the nest may result from the high level of parental synchrony when foraging. In addition we believe that synchronized activity by the parents during the breeding and non breeding seasons may help individuals to reduce vulnerability of themselves and their nests to predators.

7.6 Acknowledgements

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CHAPTER EIGHT

Nestling growth in a slightly dimorphic finch



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8.1 Abstract

Biparental care is very common in birds and through feeding rates and brood size adjustment parents can exert control over nestling growth rates. Growth and developmental rates vary widely among species, with those with a higher level of adult sexual dimorphism typically showing more dimorphism in nestling development of male and female nestlings. In sexually monomorphic species, where the two sexes attain the same size at maturity, it may also be adaptive if the two sexes have different growth trajectories, as this will reduce the peak load demands on the parents.

Long-tailed finches (*Poephila acuticauda*) are granivorous grassfinches endemic to the tropical north of Australia and they are slightly sexually dimorphic. Brood size is quite variable ranging from two to seven (4.3 ± 1.0) offspring, and competition between siblings also has the potential to affect growth rate and the size attained before fledging.

Here, we describe nestling growth rates and fledgling size in a wild population and determine the extent to which these variables are affected by (1) offspring sex, (2) brood sex ratio, (3) brood size and (4) hatching order, using logistic growth curves.

We found that the growth rate of later hatched offspring was similar to the rest of the brood, although delayed, and later hatched offspring did catch up with the rest of the brood. Despite the slight sexual size differences in adult long-tailed finches, we found no effect of sex on nestling growth rates or size at fledging, although a male-biased brood sex ratio affected fledging size of the whole brood. We did not find an effect of brood size on nestling growth rates. This study adds to current research on the effect of sex, hatching asynchrony and brood size on nestling growth rates in less dimorphic species.

8.2 Introduction

Parental care is expected to evolve whenever the benefits of enhanced offspring survival exceed the costs to the parents of providing care (Clutton-Brock 1991), which is especially common in birds, with bi-parental care occurring in over 90% of species (Clutton-Brock 1991). Parents can assert control on the level of care in different ways. Females can control clutch size and manipulate the competitive hierarchy among nestlings through hatching asynchrony (Ricklefs 2002), or the allocation of nutrients or hormones to eggs (reviewed in Groothuis *et al.* 2005). In addition, both males and females can influence incubation time (Martin 2002) and feeding rates (Martin 1987), which in turn might affect nestling growth rates (Remes & Martin 2002).

Birds can influence hatching intervals through parental care by determining when to begin incubation (Stoleson & Beisinger 1995), thereby creating size hierarchies within their brood. The first hypothesis to attempt to explain hatching asynchrony suggests it can provide parents with the opportunity to adjust their brood size to fit food availability (Brood Reduction Hypothesis; Lack 1947). Many new hypotheses have been developed since then (e.g. Magrath 1990). The peak load reduction hypothesis is one of them and suggests that the food demand of the brood is spread out to reduce energy expenditure by the parents (Stoleson & Beisinger 1995).

Another potentially important determinant of individual growth rate is the effect of offspring sex, which has been demonstrated with sexual dimorphism of nestlings in numerous avian species that have sexually dimorphic adults (e.g. Torres & Drummond 1999; Daunt *et al.* 2001; Badyaev *et al.* 2006). In sexually monomorphic species, where the two sexes attain the same size at maturity, it may also be adaptive if the two sexes have different growth

trajectories, as this will reduce the peak load demands on the parents. For example, if females grow fast in the first part of the nestling period and males grow fast in the later period of the nestling phase then across a brood with an approximately even sex ratio, the peak demand of the sons and daughters will differ. To date very few studies (e.g. Nisbet & Szczys 2001; Becker & Wink 2003; Rosivall *et al.* 2010) have empirically assessed the extent to which male and female offspring may differ in their growth rates to lighten the peak load of parents in sexually monomorphic species. In addition to sex-related peak load reduction, there might also be adaptive reasons for the sexes to differ in response to environmental conditions. For example, in the size sexually monomorphic zebra finch *Taeniopygia guttata* numerous studies have revealed that female nestlings are more adversely affected by poor conditions than male nestlings (Kilner 1998; Rutkowska & Cichón 2002; Martins 2004; Arnold *et al.* 2007), while male and female nestling collared flycatchers *Ficedula albicollis* were affected differently in reduced and enlarged broods (Rosivall *et al.* 2010). In several species in which the adults are sexually monomorphic by size, a difference at the time of fledging has been noted (Becker & Wink 2003; Zielinska *et al.* 2010).

Brood size is predicted (Godfray & Parker 1992) to have an important effect on the extent of sibling competition and hence offspring growth rates, with evidence found through comparative analysis (Royle *et al.* 1999). However, within single avian species an effect of brood size on growth rate has been found in some species (e.g. Nur 1984; Singer & Yom-Tov 1988), but not in others (e.g. Scheurlein & Gwinner 2006). Part of the reason for the inconsistency is that because of the costs of reproduction to adults (e.g. Lessells 1986) we might expect females to optimize clutch size to the ability of parents to raise that number of offspring (e.g. Pettifor *et al.* 1988). Therefore larger broods will be reared by parents that are capable of rearing a higher number of offspring, and those offspring will match the size and growth rate of those reared in smaller broods. This optimization of brood size has now been

experimentally demonstrated in numerous avian species, which by experimentally enlarging or reducing brood size and disrupting the natural correlation between parental quality and brood size such studies have shown that enlarged broods grow at different rates (slower, e.g. Gebhardt-Henrich & van Noordwijk 1994; or faster, e.g. Tschirren *et al.* 2009) and produce smaller offspring (e.g. Gebhardt-Henrich & van Noordwijk 1994; DeKogel 1997; Kunz & Ekman 2000; Tschirren *et al.* 2009).

Here we present work on an endemic Australian grassfinch, the long-tailed finch (*Poephila acuticauda*), a close relative, and ecologically similar to the widely studied zebra finch. Although they are generally considered a sexually monomorphic species, recent work has demonstrated slight sexual dimorphism in a number of ornamental traits so that in a multivariate analysis the two sexes can be reliably distinguished (Van Rooij & Griffith 2010). Here, in a species where the sexes reach the same size at maturity, but differ slightly in the expression of putatively sexually selected ornamental traits, we ask whether there is any evidence for different growth patterns of male and female offspring. We also investigate whether the variation in brood size that occurs naturally affects nestling growth rates and size attained at maturity. Finally we investigate the degree to which asynchronous hatching occurs in this species and its effects on nestling growth.

8.3 Methods

A breeding population of long-tailed finches was studied near Wyndham, Western Australia (S15°33'38", E128°08'59") from March-September 2009. Long-tailed finches are socially monogamous and pair bonds in this species are strong and last across multiple years with no evidence of divorce in this species (Zann 1977; Van Rooij & Griffith 2011). They are primarily granivorous, but supplement their diet with invertebrates (Higgins *et al.* 2006).

They nest in cavities but can also build freestanding nests and readily breed in established nest-boxes (Van Rooij & Griffith 2011). Both members of the pair contribute to nest building, the incubation of the eggs and nestling provisioning (Higgins *et al.* 2006; Van Rooij & Griffith 2011). A pair can raise several broods successfully per season, with brood sizes varying from two to seven (4.3 ± 1.0 ; Van Rooij & Griffith 2011). Incubation begins once the last egg is laid and after an incubation period of about 13.8 (± 2.5) days the nestlings hatch and stay in the nest till they fledge at about 20.5 (± 2) days old (Van Rooij & Griffith 2011).

Nestling growth rates

Nestboxes were monitored every six days to identify the start of breeding attempts. When at least one egg was found, boxes were monitored more intensively to identify the clutch size and, by deduction, the first egg date and expected hatch date. From a day before the expected date the boxes were checked daily (early morning) to get the exact hatching day of each egg (day 0). At hatching nestlings are sparsely covered in white-grey down and their eyes are closed. The first feathers emerge through the skin around 7-8 days; the eyes also open around this time, and nestlings are fully feathered around day 16 (Van Rooij pers obsv). To allow individual recognition (by the observer) of nestlings, the offspring's claw (on one toe, at the very end) was clipped at two-days old. Four measurements of each nestling were then taken every other day up until day 16: (1) body mass (g); (2) tarsus length (mm); (3) combined head and bill length (mm) (from the back of the head to the tip of the bill); (4) feather length of the 2nd tail feather (mm). All nestlings were measured between 6am and 10am. The measurements observed were obtained using digital callipers (0.01 mm) and with a digital scale (0.01g). When 12-days old, the nestlings were banded with an individually numbered metal band (supplied by the Australian Bird and Bat Banding Scheme. Nestlings were first measured on day two, therefore this is used as 'hatch size'; they were last measured at day 16

which is here called ‘fledging size’. Nests were not visited again after day 16 due to the risk of pre-fledging the nestlings, which tend to fledge naturally around 20.5 (± 2) days old. A small blood sample was taken for molecular sexing and stored in 95% ethanol. All individuals were sexed using the molecular sex markers P2 and P8, a well-established technique (Griffiths *et al.* 1998) that has been successfully used before for this species (Van Rooij & Griffith 2009, 2010).

Analysis

Growth of the morphological characters of nestlings was analysed using Non-Linear Regression, following the analyses of Ricklefs (1967), using SPSS v17.0 statistical package. Growth parameters (A, K and t_i) were derived for individual nestlings by fitting logistic models of the formula:

$$W(t) = A / (1 + e^{-K(t-t_i)})$$

where $W(t)$ is the size of each character at time t , A is the asymptotic size, K is a measure of ‘growth rate’ and t_i the inflection point on the growth curve. Growth curves for mass, tarsus, head bill and feather length were calculated for each nestling. Asymptotic size is therefore a predicted size they are expected to reach about 14 days after they were last measured.

Growth rate data were collected from 270 nestlings from 69 broods, with brood size ranging from two to seven (mean \pm se; 4.3 ± 1.0). Of these, we determined the sex of 82 female and 83 male nestlings in 40 complete broods to determine the effect of sex. In analyses where sex is not taken into account, all 270 nestlings are used and in the analyses with sex the 165 sexed nestlings were used.

Partial brood mortality occurred in eight nests out of 69 nests with a total of 9 out of 270 nestlings dying between hatching and fledging (i.e. 3.3%). Most partial brood mortality occurred before the age of five days, with only two offspring dying at a later time.

The effect of laying date (GLM with brood size and sex as covariates) did not affect growth rate parameters and size near hatching and fledging ($F_{59,182} = 0.357-3.799$, $p=0.106-0.988$) and was not included in further analyses. Effect of sex on nestling size (hatch and fledging size) and nestling growth (parameters A, K and ti) was tested with paired-sample t-tests of averaged female and male values within broods. Effect of brood sex ratio on size and growth parameters was assessed with spearman correlations. Effect of brood size was assessed with GLM.

All nestlings normally hatched within 24-36 hours of the first hatchling in the brood. Hatching was considered asynchronous when eggs hatched over 48 hours later than the first egg. Effect of later hatching on nestling size (fledging size) and nestling growth (parameters A, K and ti) was tested with paired-sample t-tests of the later hatched nestling and the averaged rest of the brood. Variation in size and growth parameters within broods was assessed by calculating a coefficient of variation (%CV; stdev/mean) for each brood separately ($n=40$; nestling sex not taken into account). Variation in size and growth parameters across broods was assessed for each sex separately by calculating a CV for each measure.

Table 8.1. Size and growth parameters of male and female long-tailed finch nestlings.

Individual nestling growth patterns were analysed using General Linear Mixed Models of the form; $\text{size} = A/(1 + e^{-K(t-t_i)})$, where A is the asymptotic size, K a measure of 'growth rate' and t_i is the inflection point. Size at hatching (day 2) and size near fledging (day 16) is also given. Data for each parameter is grouped by measured body part with mean \pm se (n). Size and growth parameters of male and female nestlings were compared using paired samples t-tests within each brood (for 40 broods). A Bonferroni correction for multiple (19) comparisons lowers α to 0.0026.

	Male	Female	t	df	p
Tarsus					
A	17.17 \pm 1.73 (89)	17.12 \pm 2.02 (100)	-0.382	39	0.705
K	0.24 \pm 0.03 (89)	0.23 \pm 0.04 (100)	-0.118	39	0.907
ti	6.97 \pm 1.84 (89)	7.10 \pm 1.84 (100)	0.617	39	0.514
hatch size	4.45 \pm 0.51 (80)	4.42 \pm 0.51 (96)	-1.720	39	0.093
fledging size	14.65 \pm 0.73 (80)	14.50 \pm 0.75 (92)	-1.652	36	0.107
Mass					
A	12.29 \pm 2.65 (86)	11.93 \pm 2.23 (102)	-1.513	40	0.138
K	0.28 \pm 0.05 (86)	0.28 \pm 0.05 (102)	0.449	40	0.656
ti	9.62 \pm 2.75 (86)	9.39 \pm 2.06 (102)	-0.553	40	0.583
hatch size	1.40 \pm 0.42 (80)	1.39 \pm 0.35 (96)	-1.148	40	0.258
fledging size	9.87 \pm 1.21 (80)	9.86 \pm 1.12 (92)	-2.23	36	0.032
Head-bill					
A	24.24 \pm 3.70 (83)	25.04 \pm 3.16 (95)	-0.319	39	0.752
K	0.26 \pm 0.87 (83)	0.214 \pm 0.07 (95)	-1.057	39	0.297
ti	5.17 \pm 2.65 (83)	5.50 \pm 2.45 (95)	-0.083	39	0.934
hatch size	10.22 \pm 0.66 (78)	10.28 \pm 0.63 (96)	-1.37	36	0.179
fledging size	19.77 \pm 0.73 (78)	19.66 \pm 0.77 (90)	-2.292	35	0.028
Feather					
A	16.24 \pm 3.51 (68)	16.43 \pm 3.87 (86)	0.066	33	0.947
K	0.61 \pm 0.14 (68)	0.61 \pm 0.19 (86)	0.638	33	0.528
ti	13.02 \pm 1.10 (68)	13.05 \pm 1.09 (86)	1.703	33	0.098
fledging size	13.21 \pm 2.78 (68)	13.46 \pm 2.62 (84)	-0.048	33	0.962

8.4 Results

Effect of sex on nestling size

Hatch size of offspring tarsus was 4.45mm for males (± 0.51 ; 29.4% of adult male tarsus; 15.14mm ± 0.04) and 4.42mm ± 0.51 for females (29.6% of adult female tarsus; 14.92mm ± 0.05). Hatch size of offspring mass was 1.40g ± 0.42 for males (10.1% of adult male mass; 14.16 ± 0.08 g) and 1.39g ± 0.35 for females (10.3% of adult female mass; 14.26 ± 0.11 g). Hatch size did not differ between males and females for tarsus, mass or head-bill length (Table 8.1).

Fledging size of offspring tarsus was 14.65 ± 0.73 for males (96.8% of adult male size) and 14.50 ± 0.75 for females (97.2% of adult female size). Offspring mass was 9.87 ± 1.21 g for males (69.7% of adult male mass) and 9.86 ± 1.12 for females (69.1% of adult female mass). Fledging size did not differ for tarsus, mass, head-bill or feather length (Table 8.1).

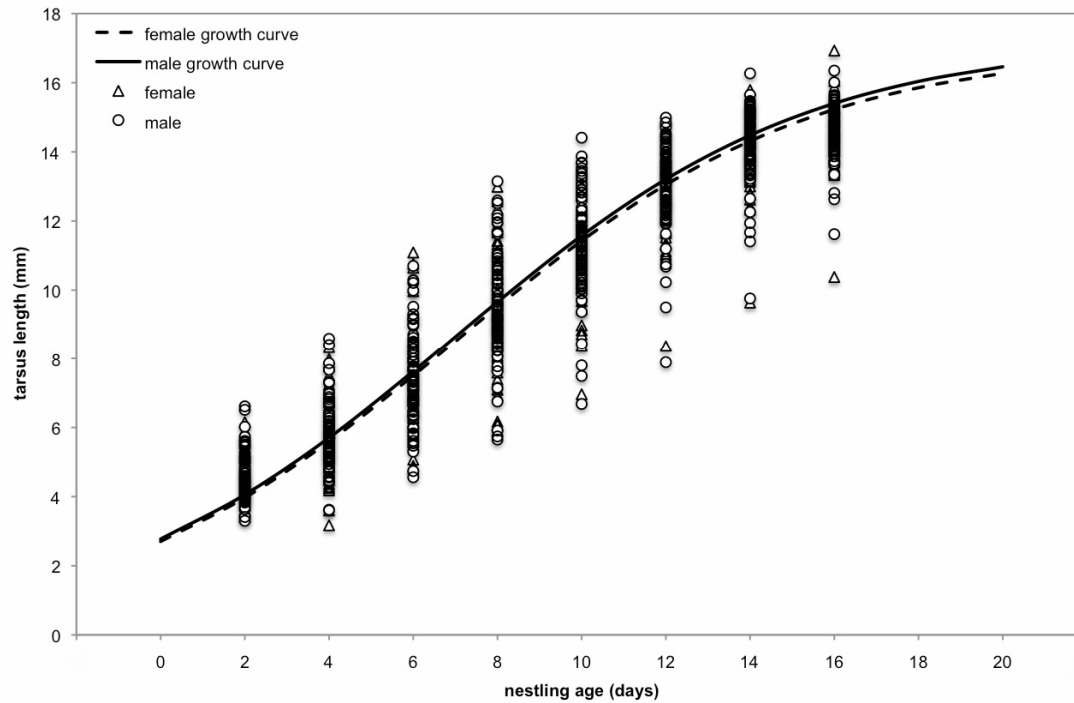


Figure 8.1a Growth curves for tarsus length for male and female long-tailed finch nestlings.

Growth curves for tarsus of long-tailed finch nestling males (line; open circles) and females (dotted line; open triangles) nestlings as fitted to a logistic model of the form: $\text{size} = A/(1 + e^{-K(t-t_i)})$, where A is the asymptotic size, K a measure of 'growth rate' and t_i is the inflection point. Measures of all nestlings for tarsus length and mass (average asymptotic size (A), growth rate (K) and inflection point (t_i) are shown in Table 8.1).

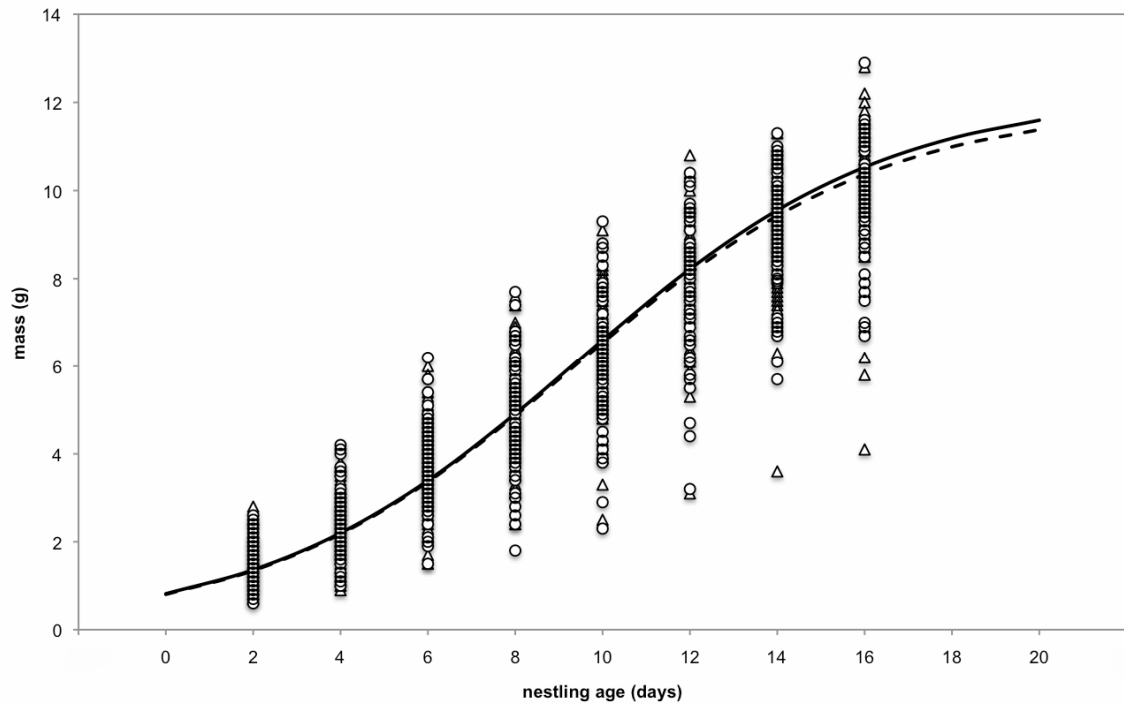


Figure 8.1b Growth curves for mass for male and female long-tailed finch nestlings.

Growth curves for mass of long-tailed finch nestling males (line; open circles) and females (dotted line; open triangles) nestlings as fitted to a logistic model of the form: $\text{size} = A/(1 + e^{-K(t-t_i)})$, where A is the asymptotic size, K a measure of 'growth rate' and t_i is the inflection point. Measures of all nestlings for tarsus length and mass (average asymptotic size (A), growth rate (K) and inflection point (t_i) are shown in Table 8.1).

Table 8.2. Brood sex ratio and brood size.

Comparison of size and growth parameters of male and female long-tailed finch nestlings for brood sex ratio and brood size. Individual nestling growth patterns were analyzed using General Linear Mixed Models of the form; $\text{size} = A/(1 + e^{-K(t-t_i)})$, where A is the asymptotic size, K a measure of ‘growth rate’ and t_i is the inflection point.

The effect of brood sex ratio was analyzed with Spearman correlations. The effect of brood size was assessed by comparing all male and female nestlings in all brood sizes with a GLM (no interaction of brood size and sex; brood size * sex $p > 0.05$). A Bonferroni correction for multiple (19) comparisons lowers α to 0.0026.

Tarsus	GLM Brood Size		Brood Sex Ratio		
	F	p	r	p	n
A	0.878	0.479	-0.062	0.437	162
K	0.824	0.512	0.048	0.547	162
ti	0.363	0.835	-0.058	0.466	162
fledging size	1.232	0.301	0.016	0.850	148
hatch size	1.066	0.376	0.051	0.524	159
Mass					
A	1.992	0.100	-0.181*	0.022	161
K	1.554	0.191	-0.066	0.406	161
ti	1.890	0.116	-0.077	0.335	161
fledging size	1.299	0.274	-0.197*	0.016	148
hatch size	2.607	0.039	0.046	0.566	159
Head-bill					
A	0.677	0.609	-0.114	0.162	151
K	0.505	0.732	0.098	0.232	151
ti	0.802	0.526	-0.043	0.599	151
fledging size	2.844	0.027	-0.164*	0.050	144
hatch size	2.767	0.030	-0.105	0.216	141
Feather					
A	2.166	0.077	-0.251**	0.004	127
K	2.150	0.079	0.077	0.393	127
ti	0.622	0.648	0.099	0.270	127
fledging size	1.986	0.101	-0.341**	0.000	123

Effect of sex on nestling growth

No significant effect of offspring sex was discovered on the shape of the growth curves, expressed by asymptotic size (A), growth rate (K) or inflection point (t_i) for tarsus length (Figure 8.1a), mass (Figure 8.1b), head-bill size, or feather development.

There was no sex difference in growth rate (K) or asymptotic size (A) for tarsus, mass, head-bill length, or feather length (Table 8.1). To grow from 10% to 90% of the asymptote nestlings needed 16.2 / 16.2 (female/male) days for tarsus, 17.1 / 17.2 (female/male) days for mass, 20.3 / 18.2 (female/male) days for head-bill length and 16.9 / 16.7 (female/male) days for feather length.

There was no sex difference in timing of fastest growth (inflection point t_i) for tarsus, mass, head-bill length, or feather length (Table 8.1). The time of the fastest growth did differ between the different body measures for males (Paired t-tests between all measures; $t_{35-40} = 5.499-10.583$, $p < 0.001$) as well as females ($t_{33-39} = 7.849-24.878$, $p < 0.001$), with head-bill development first (male day 5.17 ± 2.65 ; female 5.50 ± 2.45), followed by tarsus (male 6.97 ± 1.84 ; female 7.10 ± 1.84) and mass (male 9.62 ± 2.75 ; female 9.39 ± 2.06) and lastly plumage development (male 13.02 ± 1.10 ; female 13.05 ± 1.09).

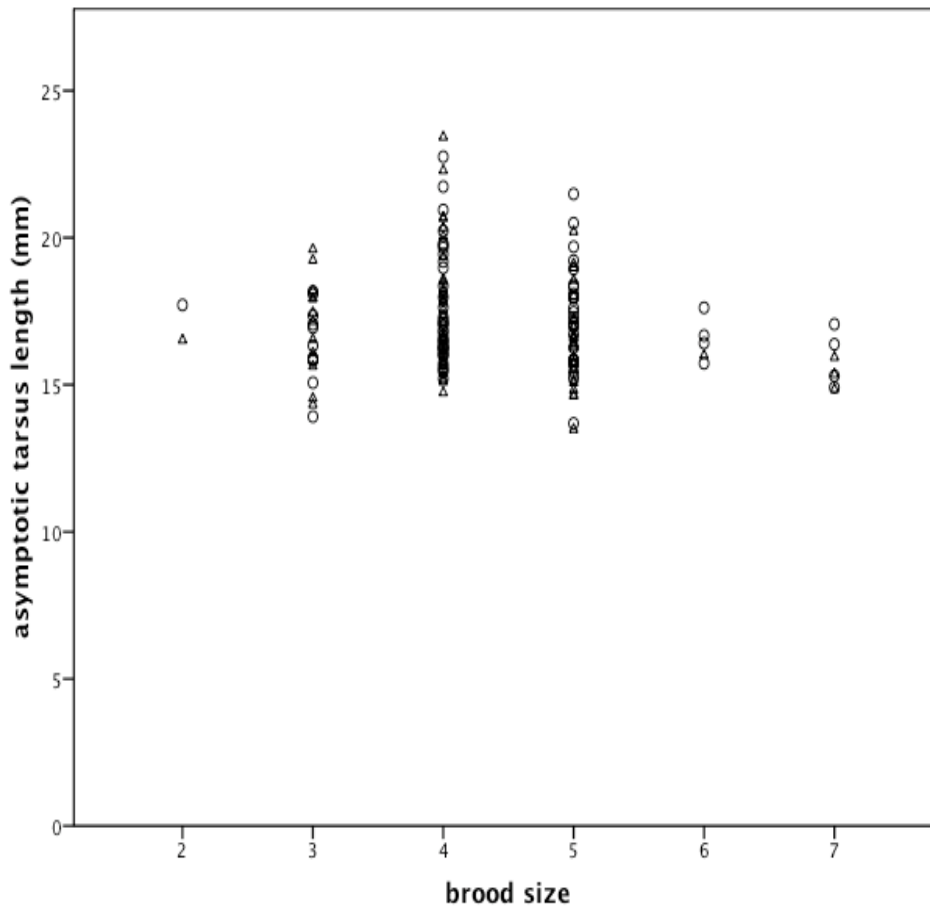


Figure 8.2a Optimal brood size for tarsus asymptotic size.

Asymptotic size of males (open black circle) and females (open black triangle) for tarsus for all brood sizes.

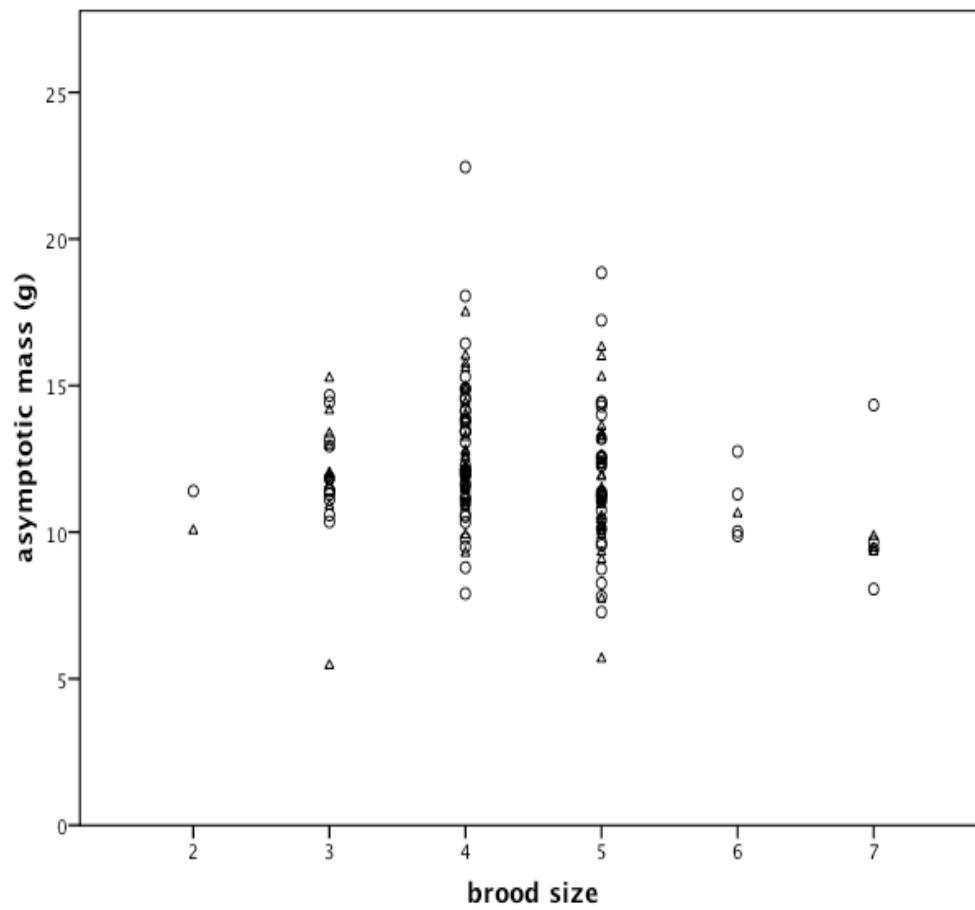


Figure 8.2b Optimal brood size for asymptotic size.

Asymptotic size of males (open black circle) and females (open black triangle) for mass for all brood sizes.

Table 8.3. Size and growth of last hatched nestlings compared to the rest of the brood.

Size of last hatched nestlings ('last') compared to the rest of the brood ('rest') from hatching till fledging and growth parameters. Last hatched nestlings were compared with the average of the rest of the brood with paired-samples t-tests. A Bonferroni correction for multiple (16) comparisons lowers α to 0.003.

	Day										
Tarsus	hatch	4	6	8	10	12	14	fledge	K	A	ti
rest	4.37	5.57	7.65	9.56	9.97	11.18	11.90	12.44	15.60	0.28	6.02
last		4.07	5.22	6.63	7.41	9.02	10.72	11.47	18.04	0.21	10.32
% dif		26.92	31.80	30.61	25.73	19.30	9.88	7.85			
F								-1.79	-3.17	1.72	8.53
p								0.13	0.03	0.15	0.00
Mass											
rest	1.43	2.25	3.64	4.94	5.16	6.29	7.45	7.80	11.03	0.29	8.80
last		1.13	1.90	2.92	3.17	4.41	6.30	7.14	11.87	0.28	12.29
% dif		49.90	47.84	40.88	38.52	29.89	15.40	8.46			
F								1.38	-0.71	0.70	6.69
p								0.23	0.51	0.52	0.00
Head-bill											
rest	7.00	8.02	9.12	10.32	11.39	15.19	15.98	16.64	22.13	0.20	4.58
last		6.92	7.76	8.72	9.90	13.02	14.54	15.82	22.40	0.19	7.02
% dif		13.77	14.83	15.58	13.05	14.29	9.01	4.89			
F								-1.82	-0.24	0.10	2.12
p								0.13	0.82	0.92	0.09
Feather											
rest				0.50	1.62	3.38	5.55	7.00	14.37	0.64	12.70
last						0.65	2.61	4.45	12.11	0.98	14.12
% dif						80.66	53.03	36.46			
F								-3.42	1.87	-0.38	2.35
p								0.08	0.2	0.74	0.14

Effect of brood size

Brood size did not affect growth rate (K), asymptotic size (A) and inflection point (ti) for tarsus, mass, head-bill and feather length, only fledging head-bill length and fledging mass and hatching head-bill seem to be affected by brood size (Table 8.2). Nestling sex did not influence the effect of brood size (brood size*sex $F=0.737$, $p=0.948$). Despite a lack of a clear difference between brood sizes, there seems to be an optimum brood size for e.g. asymptotic size (Figure 8.2a and b).

Effect of brood sex ratio

Brood sex ratio was 1:1 in 11 nests (28%), male biased in 16 nests (40%) and female biased in 13 nests (33%). A higher ratio of males in a brood negatively affected nestling growth rates and fledging size (GLM $F=2.054$, $p=0.000$; Table 8.2), specifically for fledging mass ($r=-0.197$, $p<0.05$), fledging head-bill ($r=-0.164$, $p=0.05$), fledging feather length ($r=-0.341$, $p<0.001$), asymptotic mass ($r=-0.181$, $n=161$, $p<0.05$) and asymptotic feather length ($r=-0.251$, $n=127$, $p<0.005$), however when applying a Bonferroni correction this effect is no longer significant.

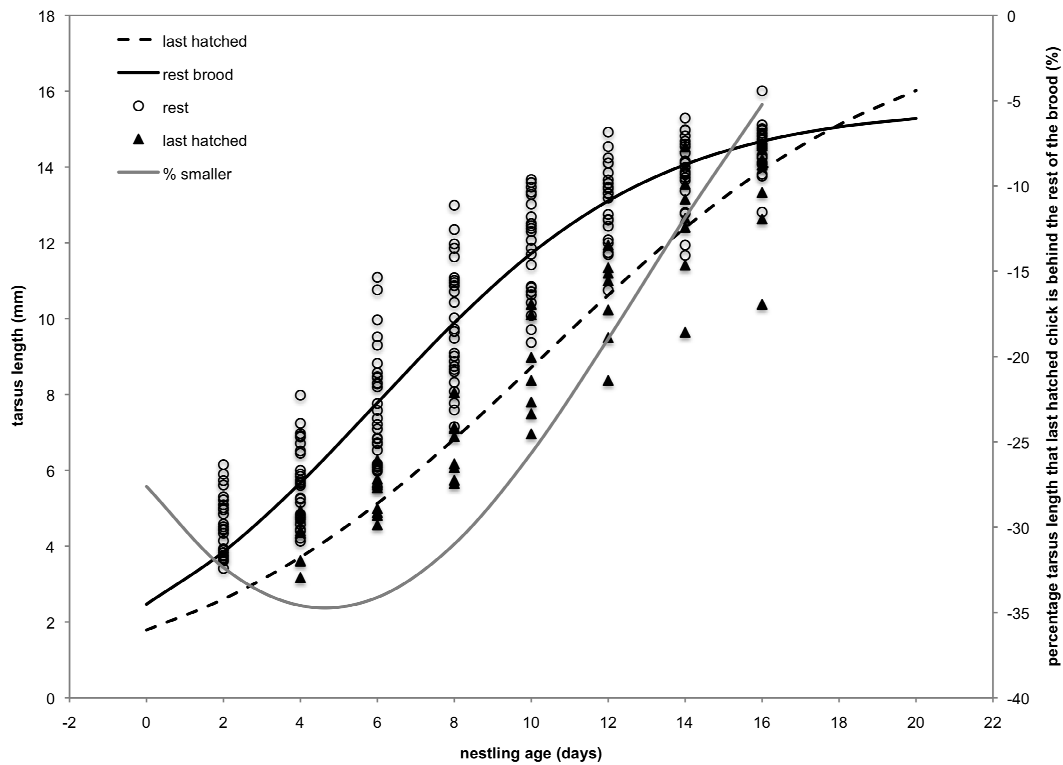


Figure 8.3a Size and growth curves last hatched nestlings compared to the rest of the brood.

Size and growth curves for tarsus length of long-tailed finch last hatched (dotted line; open triangles) nestlings and the rest of the brood (solid line; open circles) and as fitted to a logistic model of the form: $\text{size} = A/(1 + e^{-K(t-t_i)})$, where A is the asymptotic size, K a measure of 'growth rate' and t_i is the inflection point. Measures of all nestlings for tarsus length and mass (average asymptotic size (A), growth rate (K) and inflection point (t_i) are shown in table 8.3). The grey line shows the size difference (%) between the last hatched nestling and the rest of the brood.

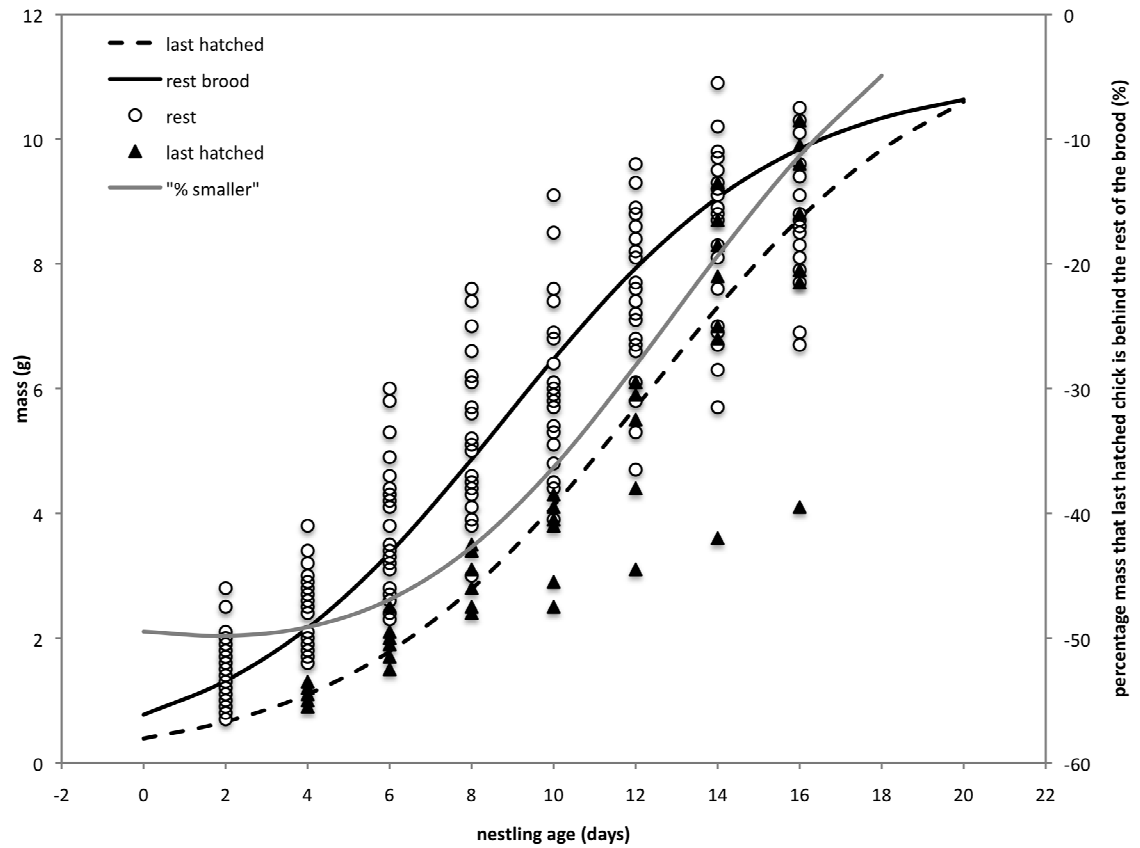


Figure 8.3b Size and growth curves last hatched nestlings compared to the rest of the brood.

Size and growth curves for mass of long-tailed finch last hatched (dotted line; open triangles) nestlings and the rest of the brood (solid line; open circles) nestlings as fitted to a logistic model of the form: $\text{size} = A/(1 + e^{-K(t-t_i)})$, where A is the asymptotic size, K a measure of 'growth rate' and t_i is the inflection point. Measures of all nestlings for tarsus length and mass (average asymptotic size (A), growth rate (K) and inflection point (t_i) are shown in table 8.3). The grey line shows the size difference (%) between the last hatched nestling and the rest of the brood.

Table 8.4. Coefficient of variation (%CV) for all size and growth parameters within and across broods.

For within broods mean %CV, minimum and maximum %CV-values (n=40 broods). Across broods (n=40) for female and male separately.

Tarsus	Within broods	Across broods	
	MEAN % CV	Female % CV	Male % CV
A	6.4	8.0	7.6
K	11.1	13.9	11.2
ti	17.9	17.7	20.7
hatch	9.0	10.2	10.9
fledging	2.9	4.7	3.9
Mass			
A	9.7	23.9	17.0
K	10.0	21.9	13.1
ti	14.7	23.5	21.5
hatch	20.5	19.8	26.4
fledging	6.1	13.7	11.2
Head-bill			
A	9.5	21.3	9.2
K	19.8	28.5	27.0
ti	33.7	46.0	38.5
hatch	5.3	4.9	5.8
fledging	2.9	3.8	2.8
Feather			
A	17.3	19.2	17.5
K	19.9	26.3	15.6
ti	6.6	5.6	6.4
fledging	13.8	16.0	16.8

Variation within and across broods

In each brood, the last hatched nestlings did not differ from the rest of the brood in fledging size, asymptotic size and growth rate ($n=7$ broods; Table 8.3). They did however reach the point of fastest growth (inflection point) later than the rest of the brood for both tarsus and mass (Figure 8.3a and b). The difference in size between last hatched nestlings and the rest of the brood varied during the nestling phase and declined from day six for tarsus and day four for mass (Table 8.3; Figure 8.3). Last hatched nestlings were predicted by the growth curves to catch up with the rest of the brood at day 18 for tarsus length and on day 20 for mass.

Fledging size and hatch size were least variable within and across broods (Table 8.4). Asymptotic size (A) was slightly more variable, as was growth rate (K). Inflection point (ti) was most variable within broods as well as across broods.

For all measures (tarsus, mass, head-bill and feather) chicks that grew more slowly reached a higher and later asymptote (Table 8.5). Hatch and fledging size were also correlated for tarsus, head-bill and mass (Table 8.5).

Table 8.5. Correlations between growth rate (K), asymptotic size (A), inflection point (ti), hatch size and fledging size.

Tarsus	A - K	A - ti	K - ti	hatch - fledging
rs	-0.720**	0.810**	-0.804**	0.182*
p	0.000	0.000	0.000	0.011
n	243	243	243	193
Mass				
rs	-0.623**	0.790**	-0.703**	0.182*
p	0.000	0.000	0.000	0.011
n	238	238	238	193
Head-bill				
rs	-0.913**	0.828**	-0.748**	0.479**
p	0.000	0.000	0.000	0.000
n	219	220	219	164
Feather				
rs	-0.761**	0.377**	-0.315**	
p	0.000	0.000	0.000	
n	169	169	169	

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

8.5 Discussion

In this study we described nestling growth rates and fledging sizes in the slightly dimorphic long-tailed finch. We found that later hatched offspring have a similar but delayed growth curve compared to the rest of the brood but do catch up with the rest of the brood before fledging. This spreads the energy expenditure for the parents (Peak Load Reduction; Stoleson & Beissinger 1995). Perhaps surprisingly, offspring sex and size of the brood did not affect nestling growth rates or size at fledging.

The pattern in which nestling birds hatch is controlled by their parents through the timing of the onset of incubation (Magrath 1990). Hatching asynchrony is a common phenomenon amongst altricial birds, and in the long-tailed finch it occurred in only a small percentage of broods (18%). Although from the offspring perspective, hatching asynchrony results in age and size hierarchies within broods, for parents it spreads out the demands for food by individual offspring (Peak Load Reduction; Stoleson & Beissinger 1995). Last hatched offspring were not more or less likely to be males or female, which is consistent with the lack of difference in size between the two. Last hatched nestlings in this species followed a similar growth curve to the rest of the brood, but were delayed in reaching the point of fastest growth (inflection point) for tarsus and mass, which is similar to what was found for the barn swallow *Hirundo rustica* (Mainwaring *et al.* 2009). The difference in size between last hatched offspring and the rest of the brood decreased progressively though the nestling phase and last hatched offspring caught up in size with the rest of the brood before fledging. Although this finding suggests that spreading the peak load during parental provisioning may be advantageous to parents, the effect is quite limited and actually does not occur in another context in which it may also make sense – peak load asynchrony of the two sexes.

In sexually monomorphic species, where the two sexes attain the same size at maturity, it may also be adaptive if the two sexes have different growth trajectories, as this, like hatching asynchrony, could also reduce the peak load demands on the parents. We did not find any effect of offspring sex on the shape of the growth curve for any of the measured variables, as was found in other less dimorphic or monomorphic species (e.g. Becker & Wink 2003; Nisbet & Szczys 2001). Asymptotic size (A), nestling growth rate (K) or timing of fastest growth (inflection point (t_i)) did not differ at all between males and females. Parents therefore are unable to spread the load by adjusting the number of males and females in their brood. We found no sex difference in size at fledging which has also been found in some other size-monomorphic species (e.g. Potti 1999; Rosivall *et al.* 2010), but not all (e.g. Zielinska *et al.* 2010). Neither did we find much variation within broods, suggesting parents manage to create broods with equal size, able to fledge at the same time. The slight sexual size dimorphism in adults of this species (Van Rooij & Griffith 2010) must therefore be established between fledging and maturity (at around 60-80 days of age). To assess whether there are differences between the sexes in response to environmental conditions, as has been reported in some other size-monomorphic species (e.g. zebra finch Martins 2004; Arnold *et al.* 2007; blue tit Dubiec *et al.* 2006), manipulative studies would be needed. Although males and females did not differ in fledging size, a higher ratio of males in broods did affect asymptotic size and the fledging size of the whole brood. A higher ratio of males in the brood also reduced the length of tail feathers in their female siblings. This does potentially provide some evidence of differences between male and female offspring with perhaps male-biased broods being more competitive social environments in which to grow. The alternative possibility is that this pattern was correlated with adult traits that are related to the production of sex-biased broods. For example, in some avian species brood sex ratios are related to maternal condition (Thuman *et al.* 2003) or male ornamentation (Sheldon *et al.* 1999).

Brood size is predicted (Godfray & Parker 1992) to have an important effect on the extent of sibling competition and hence offspring growth rates, but we found that brood size did not affect any of the growth measures or final nestling size. Because of the costs of reproduction to adults (e.g. Lessells 1986) we might expect females to optimize clutch size to the ability of parents to raise that number of offspring (e.g. Pettifor *et al.* 1988), which is exactly what our data suggests. We also found no interaction between brood size and offspring sex, showing males and females did not react differently to an increased level of sibling competition.

In summary, our results show that delayed hatching of some offspring allows parents in this slightly dimorphic species to increase their brood size while spreading the load of raising additional offspring. Further research is required to study hatching asynchrony in this species in more detail. We also found that sex did not affect the shape of the growth curves and therefore does not provide a mechanism for parents to spread the load. Brood size did not affect growth parameters caused by parents adjusting brood size to fit their own ability to raise offspring. This study provides another example of a slightly dimorphic species in which nestling sex appears not to affect nestling growth rates.

8.6 Acknowledgements

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CHAPTER NINE

General Discussion



This study contributes to our understanding of how sexual selection occurs in birds, by reporting data on a new species, the long-tailed finch - a species with multiple putative ornaments in both sexes and clinal variation in one of them – and thus makes a contribution to the body of literature that can be used in future work to make significant synthesis that changes our understanding. This family of birds (the Estrildid finches) is currently poorly represented in the literature in a region of the world (Australia) in which there have been relatively few intensive studies of sexual selection in the wild.

Breeding ecology

Through our intensive field research of a breeding population of the Long-tailed Finch, we have been able to describe for the first time some of the important reproductive parameters of one of the more common Estrildid finches occurring in the tropical northern savannah of Australia (Chapter 2). This basic data is important to further our understanding of Australian biodiversity. Even for a family as well recognised as the Estrildid finches there have been surprisingly few studies of most species. The Long-tailed Finch makes an interesting and important contrast with the closely related, but ecologically different zebra finch, which has now become one of the most important avian model systems in the world (Griffith & Buchanan 2010). Previously Zebra Finches have been conceptualised as being a laboratory model similar to other small passerines, well studied in the wild like house sparrows and blue tits, which are so phylogenetically and ecologically different it is difficult to make comparisons. However, here we have shown that while the Zebra Finch is very different to most of those birds, it is very similar to a closely related Australian Finch living in a different ecological setting. This study is also important in providing a contrast with the Gouldian Finch, which is ecologically similar whilst being in decline while the Long-tailed Finch is doing much better (Appendix). We found that levels of competitive interference at nest-sites

in the wild were high for Gouldian, but not Long-tailed Finches, and interference frequency only affected Gouldian Finch reproductive success (Appendix).

Use of nest boxes

Natural cavities in this area were very difficult for researchers to access as they were located high in the trees and/or at the ends of hollow branches, making it impossible in most cases to access eggs and nestlings and reliably catch parents. However, following on from a similar approach in the closely related zebra finch (Griffith *et al.* 2008), to facilitate the intensive study of the breeding ecology of this species we erected about 200 specially designed nestboxes (full details in Brazill-Boast *et al.* 2011). As with the zebra finch, the long-tailed finch very readily accepted the nest boxes, and indeed preferred them to natural sites. We are aware that the provision of nest boxes can create several biological artefacts resulting from, for example, unnatural breeding densities, nest-parasite dynamics, and reduced predation (Møller 1989). Density of nesting sites was only slightly increased in the study area by the provision of nest boxes, but this species does not only nest in natural cavities but also nests in grass nests in the foliage of trees (Immelmann 1965; Brazill-Boast *et al.* 2010), resulting in a virtually unlimited number of available nesting sites. We did find that nesting attempts in natural cavities were more likely to fail than nesting attempts in artificial nest boxes, which was also found for zebra finches breeding in nest boxes compared to free standing nests (Griffith *et al.* 2008), and in both cases was presumably due to the reduced vulnerability of nests in boxes to predation. We did not find increased clutch size and fledging success for the nesting attempts in nest boxes, however the sample size was small for attempts in natural cavities.

Ornamentation in both sexes

The Long-tailed Finch has previously been described as sexually monomorphic (Immelmann 1965; Langmore & Bennett 1999) and has provided the only solid support (Langmore & Bennett 1999) for the sexual indistinguishability hypothesis (Burley 1981), which argued that sexual monomorphism is an adaptation to avoid competition in flock-living species. Individuals might benefit by being able to conceal their sex, as repeated interactions due to sexual competition would sometimes be disadvantageous (Burley 1981). We have demonstrated that over 90% of individuals in the wild population could be reliably sexed on the basis of appearance alone and only 6% of males in this population were mistaken for females in our discriminate function analysis (Chapter 4), which provides only a very small group of males the opportunity to conceal their sex in the absence of behavioural cues. This showed that whilst the level of sexual dimorphism across a number of traits is limited, together these characters are sufficient to accurately signal the sex of an individual. Whilst it is possible that on a quick visual inspection the sexes may be difficult to determine, in an appropriate ecological context it is difficult to see that concealing one's sex is either possible or adaptive in this species. We suggest therefore that the sexual indistinguishability hypothesis (Burley 1981) does not account for the similarity between males and females in this species.

Santos & Lumeij (2007) later classified this species as sexually dichromatic with respect to bill and crown colouration. The expression of several traits by the Long-tailed Finch (tail streamers, coloured bill, black throat patch) made it seem plausible to suspect they may have a signaling function, and the demonstration of multiple signals in other species (e.g. Pryke & Andersson 2005; Pryke *et al.* 2001, 2002), means that it was appropriate to account for all of them simultaneously in any investigation of sexual selection. We supported the work of

Santos & Lumeij (2007) and found variation in ornament expression within and between the sexes, with sexual dimorphism most pronounced in patch size and tail streamer length, suggesting an ornamental function (Chapter 4).

Social mate choice

In monogamous species where both sexes possess ornaments, mutual mate choice may often play an important role in the development of secondary sexual characters in both sexes (Amundsen 2000; Kraaijeveld *et al.* 2007). In this study however we found no mutual mate choice evidenced by the lack of assortative pairing with respect to variation in homologous ornaments, body size and body condition in the two sexes (Chapter 5). It is certainly possible that assortative mating does occur in this species, either infrequently or in such a weak form as to be very difficult to detect reliably. Indeed, we did find some very weak support for assortative mating by wing length, body size and patch size, although none of these findings remained significant after correcting for the number of tests we ran, and none was found in more than a single year.

In other species in which assortative mating has been identified for a particular trait, that same trait is often found to relate to an important fitness related trait such as reproductive success (e.g. Masello & Quillfeldt 2003), or individual survival (e.g. Griffith *et al.* 2003). The traits for which we found weak indications of assortative mating (wing length, body size and patch size) may all conceivably be expected to relate to fitness, and have all been found to be indicative of reproductive success in other passerine species. However, again, our analysis did not find clear indications of a role for any of these traits in predicting reproductive success.

Extra-pair mate choice

The level of sexual selection in most socially monogamous birds is largely dependent upon the level of, and distribution of extra-pair paternity (EPP) amongst males in a population. When individuals are not paired with the preferred social partner, extra-pair relations could be favoured (Albrecht *et al.* 2009), where male ornamentation might be a cue in female choice for an extra-pair mate. Therefore there is a potentially important role of extra-pair fertilizations in the evolution and / or maintenance of elaborate male ornaments in socially monogamous taxa (Albrecht *et al.* 2009). However only if males with a certain expression of ornamentation are more successful in siring extra-pair offspring than randomly selected males, then female choice of such males may be a major component of sexual selection in monogamous species (Birkhead & Møller 1992; Whittingham & Dunn 2005), especially in species like the Long-tailed Finch that form pair bonds that are maintained throughout the year and likely last for life (Zann 1977; Chapter 2). Here, (Chapter 6), we found that the Long-tailed Finch is among the species with the lowest rates of EPP of the socially monogamous passerines (Griffith *et al.* 2002), with a slightly higher percentage (6.2%) than that found for the only other studied Estrildid, the Zebra Finch, with 1.7-2.4% found in wild populations (Birkhead *et al.* 1990; Griffith *et al.* 2010). However, in the Long-tailed Finch, the percentage of broods with extra-pair paternity (17.9%) is much higher compared to the level (5-8%) found in the Zebra Finch (Birkhead *et al.* 1990; Griffith *et al.* 2010). Neither males nor females selected an extra-pair mate with a higher expression of ornamentation to sire higher quality offspring with. Extra-pair offspring did not show superior growth than other offspring. The fact that extra-pair males are ‘near neighbours’ but not usually ‘the nearest neighbour’ suggests they are not selected at random, i.e. the female is likely to have ignored a number of closer options to copulate with the male that sired EP offspring in her brood. In some other mutually ornamented species sexual selection is increased through EPP

by more ornamented males (e.g. monomorphic house martin *Delichon urbica* Whittingham and Lifjeld 1995), while in others EPP is randomly distributed with respect to male ornamentation (Hill *et al.* 1994; Kraaijeveld *et al.* 2004a).

Our findings support a growing number of studies that have failed to find any obvious support for the good genes model of EPP in birds and we suggest that the adaptive benefits of EPP to females require further investigation. Our findings suggest that the expression of these putative ornamental traits in both sexes of this species may play no current role in mutual mate selection, or as indicator traits of reproductive performance (Chapter 5 and 6).

Variation in reproductive success

Within a breeding season pairs could potentially have up to three successful nesting attempts. Reproductive success seemed to vary between individuals with pairs having one (78%), two (18%) or three (4%) recorded successful attempts per breeding season (Chapter 2), however pairs could have nested in natural cavities we were unable to reach or just outside the area we monitored, although both adults and offspring of this species are highly philopatric (Chapter 2). It is therefore impossible to get a precise measure of reproductive success of pairs. In a truly socially monogamous species the variation in reproductive success among the individuals within a population may be fairly limited, as most males and females will get the opportunity to breed, with the variance driven by differences in clutch-size and the proportion of eggs that result in fledged young. Brood size varied between pairs and breeding attempts (3.98 ± 1.10 ; 1-7; Chapter 2) and 31.8% of nests in which eggs were laid fledged any young. In this species however, clutch size and number of offspring fledged was not related to parent morphology (Chapter 5) and reproductive success seemed to be randomly distributed with respect to parent morphology. The variation in reproductive success among individuals will

be increased if EPP is non-randomly distributed within a population, with some males being particularly successful at gaining EPP at the expense of others (Webster *et al.* 1995). The occurrence of EPP in this species however seemed to be randomly distributed across males with respect to male morphology and males were not consistently getting paternity or defending paternity (Chapter 6). We cannot rule out the genetic correlation hypothesis (Lande 1980; Lande and Arnold 1985) to explain the expression of female ornaments in this species, however we have not found evidence that the male ornamentation is an indicator of reproductive success.

Importance of Pair bond

Mate fidelity was high with pairs observed breeding together multiple times per season and over multiple breeding seasons (Chapter 2). The pair bond in this species appears to be very strong and pairs were typically observed acting as a single unit with partners following each other and performing all activities simultaneously including roosting, resting, foraging and preening, as previously described by Immelmann (1965) for Long-tailed Finches and Zebra Finches and confirmed by Zann (1977). Familiarity with a long time partner might affect the success of the breeding attempts through better synchronisation of the partners. Long-tailed finches showed highly synchronous nest visit behaviour, but nest visit synchrony did not seem to increase with pair bond duration (Chapter 7), although it has been suggested that increased pair duration may allow increased familiarity between mates and therefore better coordination of parental care (Fowler 1995; Black 1996). The high degree of parental synchrony at the nest therefore may reflect the ‘togetherness’ of the couple but does not reflect the duration of the pair bond. This ‘togetherness’ may also be affected by the similarity of parental personalities which in turn may have a positive effect on reproductive success (Schuett *et al.* 2011) as well vocalizations between pair members (Elie *et al.* 2010). Neither

did pair bond duration seem to affect the occurrence of extra-pair offspring in a brood (20% extra-pair offspring among older pairs and 12.5% in new pairs; Chapter 6).

Parental care and nestling growth

Nest visit synchrony (pairs visiting the nest together to feed their offspring) is high in this species with pairs visiting the nest together in 73% of nest visits (Chapter 7), and comparable to the zebra finch (Gilby *et al.* 2011). We did find some very limited evidence that synchronized nest visits may affect the reproductive success in this species. Nest visit synchrony however can be linked to foraging synchrony as individuals often forage with their breeding partner or members of the breeding group (e.g. Zann 1996), therefore nest visit synchrony in this species could simply have developed as a side effect of the pair feeding together. Synchronization might be easier for granivorous species like the long-tailed finch because the food source doesn't move and is more predictable, compared to species that feed their young e.g. invertebrates which are more difficult to capture and locate, and therefore may not be able to synchronize nest visits. Nest visit synchrony has also been suggested to play a role in minimization of nest disturbance and reducing predator attraction (Raihani *et al.* 2010), especially in species like the long-tailed finch where the nest cavity is concealed and predators in the nest are not visible from the exterior (e.g. Doutrelant & Covas 2007). In this population breeding in nest boxes predation rates were relatively low, therefore it is highly possible that predation and halving the amount of activity around the nest is a primary selective force behind synchrony. Pairs forage together and also visit the nest together (and enter one at a time) then they can very effectively look out for one another and essentially be a sentinel for each other.

Nest visit rate (Chapter 7) was not affected by male or female ornamentation as suggested in the good parent hypothesis (Hoelzer 1989) where parental effort is correlated with ornamentation (e.g. northern cardinals *Cardinalis cardinalis* Linville *et al.* 1998; rock sparrow *Petronia petronia* Griggio *et al.* 2010). Nest visit rate was low in this species (0.77 visits per hour by each individual; Chapter 7) compared to species such as the blue tit, however similarly low nest visit rates were found in other granivorous species (e.g. 0.75 individual visits per hour in crimson rosella *Platycerus elegans* Krebs *et al.* 1999; 1.08 individual visits per hour in green-rumped parrotlet *Forpus passerinus* Budden & Beisinger 2009). Males and females provisioned the nestlings at similar rates, which is also found in several other bird species (e.g. Tremont and Ford 2000; Royle *et al.* 2006; Lee *et al.* 2010). Although nest visit rate was very low, it did increase with larger brood size.

Although Long-tailed Finches are a bi-parental species, we observed a single case of helping at the nest by a juvenile male from a previous nest in 2008, which was the first occasion that more than two individuals were recorded supplying food to nestlings in this species. This was only seen once that season and not seen in the two seasons after (2009 and 2010). We therefore certainly do not intend to suggest that the long-tailed finch should be considered a cooperatively breeding species, however, observations such as these help us to understand the variation that exists in nature with respect to familial relations and parental care and helps to provide a foundation for work addressed at understanding the evolutionary origins of cooperative behaviour in birds.

Although found in a variety of species (Naef-Daenzer and Keller 1999; Lee *et al.* 2010), we did not find a significant relationship between parental nest visit rate and nestling growth rate, presumably because parents adjusted nest visit rate with brood size and nestlings in larger broods did not receive more food than those in smaller broods fed at lower rates (Chapter 4).

Our results show (Chapter 5) that delayed hatching of some offspring allows parents in this slightly dimorphic species to increase their brood size while spreading the load of raising additional offspring. Further research is required to study hatching asynchrony in this species in more detail, as this result is based on a small sample size in a wild population which means many variables can not be controlled, e.g. predation pressure, food availability. By assessing the effect of hatching asynchrony in an aviary set-up it would be possible to assess hatching times in greater detail while at the same time creating an environment which is the same for all pairs, e.g. food supply, distance to food. We also found that sex did not affect the shape of the growth curves and therefore does not provide a mechanism for parents to spread the load. Brood size did not affect growth parameters caused by parents adjusting brood size to fit their own ability to raise offspring.

Conclusion

We are currently unable to identify any function for these very elaborate secondary sexual characters in either sex of this species and suggest that the typical general assumption that all such traits have an ornamental function may need further examination. Only for some species similar to the Long-tailed Finch, i.e. where both males and females express ornamental traits to a similar extent, it has been shown that female ornaments are quality indicators and are under direct sexual selection (e.g. barn swallow *Hirundo rustica* Møller 1993 but see Cuervo *et al.* 1996; inca tern *Larosterna inca* Velando *et al.* 2001; rock sparrow *Petronia petronia* Pilastro *et al.* 2003 and northern cardinal *Cardinalis cardinalis* Jawor *et al.* 2004; Griggio *et al.* 2005). Some other studies found assortative mating by ornamentation, which suggests mutual mate selection based on quality (Daunt *et al.* 2003; Jawor *et al.* 2003; Masello and Quillfeldt, 2003; Boland *et al.* 2004; Kraaijeveld *et al.* 2004b; Griggio *et al.* 2005). However in many other species where the function of putative ornaments has been tested it has not been

found or evidence was weak, e.g. by presenting models (Muma & Weatherhead 1989; Jones & Montgomerie 1992), correlating ornamental traits with reproductive success (Hill 1993; Daunt *et al.* 2003; Masello & Quillfeldt 2003; Veit 2003), mate choice experiments (Amundsen *et al.* 1997) or lack of assortative mating (Murphy 2008). These recent studies have provided evidence for sexually selected traits in both sexes as well as failed to find evidence of mate choice based on putative ornamental traits.

In summary, we found the multiple putative ornaments in both sexes in the Long-tailed Finch to be variable and slightly dimorphic, removing the only support for the sexual indistinguishability theory, but suggesting that these traits function as ornaments. However, we did not find evidence that the putative ornamental traits in this species were used in mutual mate selection and extra-pair mate selection. We also found no evidence that ornamental expression reflected reproductive success or parental investment. The mutual multiple ‘ornaments’ in this species therefore do not currently seem to be under sexual selection, as we are currently unable to identify any function for these very elaborate putative ornaments in either sex of this species and suggest that the typical general assumption that all such traits have an ornamental function may need further examination (see also Prum 2010). It is possible that putatively ornamental traits such as those investigated here are completely arbitrary characters that hold no information on the quality of the individual bearer other than the identification of an individual (Dale *et al.* 2001), the sex of the bearer or the species which they belong to, or that they had an important signaling role in the past which has now become redundant, leaving the traces of sexual selection in the past.

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Appendix

The work contained in this appendix is work that I was involved in which was published during my candidature. It was also published as a chapter in the PhD-thesis of James Brazill-Boast (2010).



Published as: Brazill-Boast, J., Van Rooij, E.P., Pryke, S.R. & Griffith, S.C. (2011). Interference from long-tailed finches constrains reproduction in the endangered Gouldian finch. *Journal of Animal Ecology* 80, 39-48.

Due to copyright laws, the following articles have been omitted from this thesis.
Please refer to the following citations for details.

Brazill-Boast, J.; Van Rooij, E.P.; Pryke, S.R. & Griffith, S.C. (2011).
Interference from long-tailed finches constrains reproduction in the endangered Gouldian
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FAO

Tamra Chapman

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ANIMAL RESEARCH AUTHORITY

AEC Reference No.: 2007/038

Full Approval Duration: 01 January 2008 to 31 December 2010 (36 months)

To: A/Prof Simon Griffiths
 CISAB
 Macquarie University
 Phone: (02) 9850 4186
Email: simon.griffith@mq.edu.au

Associate Investigator (s)
 Dr Sarah Pryke Phone: 9850 4187
 Ms Barbara Tschirren Phone: 9850 4187

Other people participating
 Mr James Brazil-Boast Phone: 9850 4187
 Ms Amanda Gilby Phone: 9850 4187

Is authorised by:

MACQUARIE UNIVERSITY to conduct the following research:

Title of the project: LIFE-HISTORY AND BIODIVERSITY IN FOUR ESTRILDID FINCHES: BEHAVIOUR, EVOLUTION AND CONSERVATION — IN THE WILD

Type of animal research and description of project:

Evolutionary and behavioural research - wildlife: The project will use wild finch species to investigate the evolutionary processes related to reproduction and life-history that underlie species diversity in birds. Research includes (1) mapping and characterizing variation of wild populations (individual phenotypes) (2) Breeding ecology and nest competition in the wild. Birds will be captured in the wild using mist nets. Experimental procedures include: banding (ABBBS); colour and morphological measurements; blood sampling; immunocompetence testing using PHA skin test; recording of parental care; sperm sampling; nest monitoring and observation; cross-fostering off-spring between nests. All experimental procedures to be conducted in accordance with details provided in the approved protocol.

Species of animal: Gouldian finch (*Erythrura gouldiae*); Long-tail finch (*Poephila acuticauda*); Black-throated finch (*Poephila cinerea*); Zebra finch (*Taeniopygia guttata*)

Number: Gouldian finches: up to 400 per year (total 1200); Long-tail finches: up to 600 per year (total 1800); Black-throated finches: up to 600 per year (total 1800); Zebra finches: up to 1000 per year (total 3000)

Location/s: (1) Conservation land – Wyndham Shire, North Kimberley, WA 6740
 (2) Fowler's Gap UNSW Arid Zone Research Station, via Broken Hill NSW 2880

Amendments considered by the AEC during last period: N/A

As approved by and in accordance with the establishment's Animal Ethics Committee.

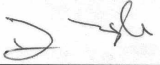
MACQUARIE UNIVERSITY AEC

Approval was granted subject to compliance with the following conditions:

(This authority has been issued as the above condition (s) has been addressed to the satisfaction of the AEC)

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

This authority remains in force from **01 January 2008** to **31 December 2008**, unless suspended, cancelled or surrendered, and will only be renewed upon receipt of a **PROGRESS** report at the end of this period.


 Dr Darren Burke
 Acting Chair of AEC, Macquarie University

Date: 12-12-07