Extra-pair paternity in the long-tailed finch *Poephila acuticauda*

Erica P. van Rooij¹, Lee A. Rollins¹,², Clare E. Holleley¹,³ and Simon C. Griffith¹

¹ Department of Biological Sciences, Macquarie University, Australia
² Centre for Integrative Ecology, Deakin University, Geelong, VIC, Australia
³ Institute for Applied Ecology, University of Canberra, Canberra, ACT, Australia

**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 surveyed socially monogamous species. We present the first molecular data on the genetic breeding system of the long-tailed finch, *Poephila acuticauda*, a grass finch endemic to the tropical northern savannah of Australia. Although the species forms socially monogamous pair bonds during the breeding season, we found that extra-pair males sired 12.8% of 391 offspring, in 25.7% of 101 broods. Our findings provide only the second estimate of extra-pair paternity in the estrildid finch family.

**Subjects** Animal Behavior, Zoology

**Keywords** Extra-pair paternity, Sexual selection, Polyandry, Infidelity, Social monogamy, Estrildid

**INTRODUCTION**

The majority of passerine birds are socially monogamous (*Cockburn, 2006*), and yet extra-pair paternity (EPP) was found to be present in over 90% of species for which paternity had been investigated when reviewed by *Griffith, Thuman & Owens (2002)*. In socially monogamous species with long-term pair bonds, both males and females are constrained in their choice of social mates by the low availability of unpaired individuals, and extra-pair mating may enable females to gain genetic benefits for at least some of their offspring (*Akcay & Roughgarden, 2007*; *Griffith & Immler, 2009*), or to secure against the infertility of a male partner (*Sheldon, 1994*; *Griffith, 2007*). In addition, focus has recently started shifting towards a number of non-adaptive models that can explain the incidence of the fairly widespread extra-pair paternity observed in many species of bird (*Forstmeier et al., 2014*).

An improved understanding of extra-pair paternity in birds will depend partly on further experimental work on well studied and amenable research species. For example, there are a handful of European and North American species that have already been the focus of dozens of studies of extra-pair paternity across multiple populations (e.g., blue tit *Cyanistes caeruleus* (e.g., *Foerster et al., 2003*); house sparrow *Passer domesticus* (*Griffith et al., 1999*); collared flycatcher *Ficedula albicollis* (*Veen et al., 2001*)). The alternative route to new insight will likely come from further comparative studies and meta-analyses that
make use of the expanding dataset on variation in extra-pair paternity across species (e.g., Cleasby & Nakagawa, 2012; Griffith, Thuman & Owens, 2002). Even in the passerines, the most extensively studied avian family, many sub-families have yet to be studied at all or have been investigated through just one or two species. To date, our understanding of extra-pair paternity in the passerine sub-family Estrildidae is based only on the study of the Australian zebra finch Taeniopygia guttata which has been the focus of two separate estimates of extra-pair paternity in the wild (Birkhead et al., 1990; Griffith et al., 2010), and numerous studies in captivity (Forstmeier et al., 2011; Baran & Adkins-regan, 2014).

The long-tailed finch Poephila acuticauda is a close relative of the zebra finch and has a similar social mating system to that species, with evidence of long-term partnerships between males and females that last across multiple reproductive attempts within and across breeding seasons (zebra finch see Zann, 1996; long-tailed finch see Van Rooij & Griffith, 2011; Van Rooij & Griffith, 2013). Here we report on a study characterizing the occurrence of extra-pair paternity in a single population of the long-tailed finch near the town of Wyndham in Western Australia. Our work is completely exploratory and we had no particular expectation of the likely level of genetic polyandry in this species, and nor were we testing any hypothesis regarding the distribution across individuals. Our study characterises the incidence of genetic polyandry by genotyping parents and offspring using microsatellite genotyping—a method that has remained the best practice for over fifteen years (Griffith, Thuman & Owens, 2002).

**METHODS**

**Study area, species and general methods**

The long-tailed finch is a common Australian grass finch of the family Estrildidae, and endemic to Northern Australia. 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 (Van Rooij & Griffith, 2011; Van Rooij & Griffith, 2013). This work focused on the western sub-species Poephila acuticauda acuticauda in an area to the west of the putative contact zone with the other sub-species P. a. hecki (Jennings & Edwards, 2005; Rollins et al., 2012). Fieldwork was conducted during three breeding seasons (March–September) in three years (2008–10) near Wyndham, Western Australia (S15°33′38″, E128°08′59″). The nominate sub-species occurs in this area, which is. The study area consisted of 108 ha of savannah woodland with Eucalypt trees providing natural cavities for nesting as well as artificial nest boxes supplied to facilitate this study and work on the Gouldian finch Erythrura gouldiae at the same site (Brazill-Boast et al., 2011).

We sampled 101 complete families (all offspring and both putative parents) over three breeding seasons (24 in 2008, 62 in 2009, 15 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, Peter & Cowling, 2006). At the age of twelve days all nestlings were banded, measured and a small blood
Table 1  Characteristics of the molecular markers used in the study. Allele size ranges, number of alleles, the level of heterozygosity, the probability of genotype sharing, probability of false inclusion, deviation from Hardy–Weinberg equilibrium and null allele frequencies, all based on the allele frequencies detected in 112 individuals (53 females, 59 males), which bred in the study area in 2008–2010.

| Locus | Allele size range | Number of alleles found | Heterozygositya | Probability of genotype sharingb | Probability of false inclusionc | Dev. from HW | Null allele frequency estimate |
|-------|-------------------|-------------------------|----------------|---------------------------------|-------------------------------|--------------|-----------------------------|
| Tgu1  | 170–192           | 10                      | 0.90           | 1.9 × 10⁻²                      | 0.19                          | Yes          | 0.0097                      |
| Tgu3  | 144–190           | 18                      | 0.95           | 5.2 × 10⁻³                      | 0.10                          | No           | 0.0679                      |
| Tgu4  | 99–147            | 19                      | 0.96           | 3.3 × 10⁻³                      | 0.08                          | No           | 0.2212                      |
| Tgu8  | 193–239           | 19                      | 0.95           | 4.5 × 10⁻³                      | 0.10                          | Yes          | 0.0417                      |
| Tgu12 | 101–139           | 16                      | 0.94           | 7.7 × 10⁻³                      | 0.12                          | No           | −0.0069                     |

Notes.

aHeterozygosity was calculated as (1 − q), where q is the mean allele frequency derived from Cervus (following Kalinowski, Taper & Marshall, 2007).
bFor a single locus the probability that two unrelated individuals will share the same genotype is given by q²(2 − q) (Kalinowski, Taper & Marshall, 2007), where q is the mean allele frequency (following Kalinowski, Taper & Marshall, 2007).
cFor a single locus the probability of false paternal inclusion is given as 2q − q² (Kalinowski, Taper & Marshall, 2007).

DNA was extracted from blood samples using the Puregene DNA Purification Kit (Qiagen). We used five fluorescently labeled 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 details of the characterization of the loci in this species are given in Table 1. All samples were run in two multiplex PCR reactions using a Qiagen Multiplex Kit at one-fifth the recommended volume, using multiplex PCRs. 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, Taper & Marshall, 2007).

We assessed the occurrence of EPP by comparing offspring with both putative parents across the microsatellite loci. Most offspring and putative parents (n = 505) were successfully scored at all five microsatellite loci, but 19 (<5%) of the 393 offspring were
scored at only four loci, because one locus failed to amplify. In the 112 adults genotyped, the loci were all highly variable ranging from 10 to 19 alleles per locus (Table 1; combined non-exclusion probabilities for this set of markers in this population were 0.012 for the first parent and 0.001 for the second parent). We used CERVUS 3.0 to assign maternity and paternity, then confirmed the output by manually comparing allele matching across loci in families. The mother was confirmed first and then maternal alleles were excluded when searching for the father. This approach combined the likelihood estimates (from CERVUS) with the more conservative traditional method of matching the inheritance of alleles at the co-dominant microsatellite loci. When social parents matched the offspring at four or more loci, in all cases, both methods concurred and we are confident of our assignment to social parents (or exclusion of social parents). In cases in which a social male was excluded, we searched the genotypes of all sampled males in the population to identify extra-pair sires. We again used CERVUS to perform a search of all males and a likelihood of assignment, and again these were compared manually for matching. In most cases the male identified as most likely by CERVUS was not considered to be the actual father on the basis of multiple mismatching loci. Paternity of extra-pair offspring was only assigned to an extra-pair male when at least four loci matched at the non-maternal allele.

RESULTS

In total, 393 offspring from 101 broods were genotyped with both their putative parents. 391 of the offspring matched with at least one of the maternal alleles at all of the loci scored. Eighty eight offspring had a mismatch with the social mother at a single maternal locus and five offspring mismatched with their social mother at two loci, but in these cases the mismatches were consistent with the presence of a null allele. i.e., the parent and/or offspring were scored as homozygotes, and most of these mismatches occurred at Tgu4 which was characterized as having a particularly high rate of null alleles. A single offspring in each of two broods mismatched with both the social mother and social father at two or more loci and these offspring were attributed to either intraspecific brood parasitism or eggs that were already in nests that were taken over by the social pair (i.e., 2 of 393, 0.5%). Mismatches between offspring and the social male occurred at a higher level (111 mismatched at one locus, 20 mismatched at two loci and 48 mismatched at three or more loci). Again, all of those with a single mismatch, and most all of those with two mismatches, could be attributed to the presence of null alleles. However, 50 of the 391 offspring (12.8 %) that belonged to the social mother at a nest were determined to have been sired by a male other than the social male at the nest, on the basis that mismatches could not be explained by the presence of null alleles. These offspring matched the social mother and we conclude that they must therefore have been the result of extra-pair paternity, and they were distributed in 26 of 101 broods (25.7%). The rates were broadly similar across the three different years (see Table 2). Of the 26 nests that contained extra-pair offspring, nine (35%) contained a single chick sired by the extra-pair male, but in 13 nests, more than half the offspring were sired by the extra-pair male with one nest containing four nestlings, none of whom were sired by the social male.
Table 2  The extra-pair paternity across years in the study population. The incidence of extra-pair paternity (EPP) in a long-tailed finch population near Wyndham, WA in 2008, 2009 and 2010. The two cases of IBP have been excluded from the total sample below.

| Year | No. of broods | No. of broods with EPP | % broods with EP nestlings | No. of nestlings | No. of EP nestlings | % of EP nestlings |
|------|---------------|------------------------|---------------------------|-----------------|-------------------|------------------|
| 2008 | 24            | 6                      | 25.0%                     | 91              | 10                | 11.0%            |
| 2009 | 62            | 16                     | 25.8%                     | 244             | 31                | 12.7%            |
| 2010 | 15            | 4                      | 26.7%                     | 56              | 9                 | 16.1%            |
| Total| 101           | 26                     | 25.7%                     | 391             | 50                | 12.8%            |

Our sample of 101 broods was produced by 59 different females, with 31 females contributing a single brood to the sample, 18 sampled across two broods, seven with three, two with four and one female sampled across five broods. The incidence of extra-pair paternity did not seem to be driven by a few individual females or males, and indeed unique pairs were sampled multiple times and may have had extra-pair paternity in one of their broods but not others (full data provided in Table S1). For individuals that were measured multiple times there did not seem to be any pattern in the incidence of extra-pair paternity over time i.e., it does not appear more likely to occur in earlier or later broods either within a year, or across years (Tables S2 and S3). For example, 23 females bred multiple times within a season, and of these 10 had extra-pair offspring in neither brood; seven had extra-pair offspring in the first but not the second; five had extra-pair offspring in the second but not the first and one had extra-pair offspring in both broods (Table S2A). It is the same kind of pattern for males breeding multiply within a season (Table S2B), and males and females breeding across two consecutive seasons (Tables S3A and S3B). Furthermore, males and females that were sampled across multiple broods were more likely to have detectable polyandry (e.g., 7 out of 31 females with one brood were polyandrous, whereas 16 out of 28 females sampled in 2 or more broods were polyandrous in at least one of their broods). However, this is as expected if there was a random distribution of polyandry across all broods—the more broods you have, the more likely you are to have polyandry in at least one of them.

An extra-pair sire was identified for just 12 of the 50 extra-pair offspring from seven of the 26 broods sired by multiple males. In five of these broods, all extra-pair offspring shared the same father, but in the other two broods, the identified extra-pair sire did not father all of the extra-pair offspring. In Table 3 we have summarized the gains and losses made by the seven males that sired extra-pair offspring in relation to additional offspring sired but also the incidence of extra-pair paternity in their own social nests. Three of the seven extra-pair sires were cuckolded themselves and overall two had fewer genetic progeny as a result of extra-pair paternity. The other five males increased their genetic output by 20–67% through the siring of additional offspring outside the pairbond.

DISCUSSION

Like so many other species of bird, and particular like many other passerines, we found that social monogamy does not always equate with genetic monogamy in the long-tailed
Table 3  The paternity gains and losses made by extra-pair sires. The gains and losses made by the seven males that were identified as extra-pair sires, both in offspring sired and offspring lost to paternity with their own social partner. The numbers reflect all of the reproductive effort that was detected and measured in the year in question.

| Male ID | Year  | EPP | EPO gained | Total offspring in social nest | No. offspring lost to EPP | Sum genetic offspring | Prop. diff. with EPP |
|---------|-------|-----|------------|-------------------------------|--------------------------|----------------------|----------------------|
| 61384   | 2008  | 2   | 2          | 1                             | 3                        | 1.50                 |                      |
| 44885   | 2009  | 2   | 3          | 0                             | 5                        | 1.67                 |                      |
| 61109   | 2009  | 1   | 5          | 0                             | 6                        | 1.20                 |                      |
| 61315   | 2009  | 1   | 7          | 2                             | 6                        | 0.85                 |                      |
| 61316   | 2009  | 2   | 15         | 3                             | 14                       | 0.93                 |                      |
| 61332   | 2009  | 2   | 5          | 0                             | 7                        | 1.40                 |                      |
| 61566   | 2009  | 2   | 5          | 0                             | 7                        | 1.40                 |                      |

In the population that we studied here, we detected a level of extra-pair paternity (13% of offspring in 26% of broods) that is very close to the average of 11% offspring in 19% of broods reported across all socially monogamous birds that were reviewed by Griffith, Thuman & Owens (2002). This finding contrasts with the only other estrildid finch that has been examined to date, the zebra finch, in which only about 2% offspring were found to be sired by extra-pair sires in two different wild populations (Birkhead et al., 1990; Griffith et al., 2010). We are confident that our overall sample size (101 broods from over 50 females), and molecular analysis provides a reasonable estimate of the level of extra-pair paternity in this species and population. However, because we did not systematically measure all of the morphological traits in adults in each of the years of study, and because our sample sizes in each year were relatively small, we were unable to explore the underlying determinants of variation in the level of extra-pair paternity across either females or males. We certainly encourage future studies of this, and other species, to accurately measure individual variation in morphological traits that may provide insight into possible selection through genetic polyandry on signals of age, attractiveness or quality.

Although we have not investigated the determinants of individual success at defending or gaining paternity, we can make some deductions about possible selection on extra-pair paternity from its incidence across individuals. For example, there is no clear pattern with respect to the incidence across a season or across years and this suggests that extra-pair paternity is not related to breeding experience or age. Individuals that had extra-pair offspring in one brood were not subsequently more likely than others to have extra-pair offspring in a subsequent brood. This suggests that there are not individual characteristics that dispose an individual to being repeatably genetically polyandrous over time.

We were unfortunately able to identify the fathers of only very few of the extra-pair offspring that we detected. This presumably reflects the fact that even though we sampled most of the birds breeding in the habitat patch in which we were working, adults appeared to range quite far out of the nesting habitat to forage, and presumably encountered many unsampled males in the broader area. The analyses and conclusions that we can draw from the few extra-pair sires that we did identify are limited. We found that all of them also had a partner with whom they bred in the same year in which they gained paternity. Although
it is possible that many of the other unidentified extra-pair sires were not breeding, which
may have been why they were not captured and blood sampled. Nevertheless, for the seven
males that we did identify, three of them lost paternity in the same year that they gained
extra-pair paternity, and two actually lost more offspring in their own nest than they gained
through their infidelity. These observations are consistent with the idea that extra-pair
paternity in this population is not strongly related to male quality. In some other passerine
species in which there are indications that extra-pair paternity is related to male quality,
it tends to be the case that the males that gain extra-pair offspring also tend to not lose
paternity in their own nests (Whittingham & Dunn, 1999).

A recent study has identified small but significant differences in the sperm morphology
of the two sub-species of the long-tailed finch, even though these are believed to have
diverged only about 0.3 mya (Rowe et al., 2015). Given these differences, it is possible that
genetic polyandry and sperm competition are involved in post-copulatory species isolation
mechanisms, and that the function of extra-pair paternity is most important in the contact
zone where the sub-species interact (Griffith, 2010). A laboratory study of another estrildid
finch did find some evidence for post-copulatory fertilisation biases across two genetically
incompatible morphs (Pryke, Rollins & Griffith, 2010). If such a process was present in
the long-tailed finch, then it may mean that there was no adaptive function to genetic
polyandry outside of the contact zone (in the area where we did this work), but may occur
because of the potential value of such behaviour in the contact zone (which is relatively
close). The fact that we have now observed some genetic polyandry in this species suggests
that this idea may be worthy of further attention.

In summary, our results provide the first estimate of the level of extra-pair paternity in
this socially monogamous species, and just the second in the family of estrildid finches.
The level of extra-pair paternity in this species is around the average level seen across all
socially monogamous birds. The incidence of extra-pair paternity across individuals in the
population does not appear to be consistently biased towards any individuals and appears
to be neither more or less likely to occur in successive broods belonging to either individual
males or females.

ACKNOWLEDGEMENTS

We would like to thank James Brazill-Boast, Belinda Cooke, Violaine Doreau, Chris
Dufresnes, Rowena Hamer, Isabelle Henry, Dhanya Pearce, Sarah Pryke, Lena Rudolph,
Marjolein Schoe, and Hanneke Wiggers, for help with the fieldwork component of this
research.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

The following grant information has been disclosed by the authors: Australian Research
Council Grant: #DP0881019, and Macquarie University Postgraduate Research Fellowship.
The funders had no role in study design, data collection and analysis, decision to publish,
or preparation of the manuscript.
Grant Disclosures
The following grant information was disclosed by the authors:
Australian Research Council: #DP0881019.
Macquarie University Postgraduate Research Fellowship.

Competing Interests
Lee A. Rollins and Simon Griffith are Academic Editors for PeerJ.

Author Contributions
• Erica P. van Rooij performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
• Lee A. Rollins and Clare E. Holleley performed the experiments, reviewed drafts of the paper.
• Simon C. Griffith conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Animal Ethics
The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):
Macquarie University Animal Ethics Committee Authorisation # 2007/038.

Field Study Permissions
The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):
The Western Australia, Department of Environment and Conservation (no. BB 002563).

Data Availability
The following information was supplied regarding data availability:
The data is presented in Tables S1–S3.

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.1550#supplemental-information.

REFERENCES

Akcay E, Roughgarden J. 2007. Extra-pair paternity in birds: review of the genetic benefits. Evolutionary Ecology Research 9:855–868.

Baran NM, Adkins-regan E. 2014. Breeding experience, alternative reproductive strategies and reproductive success in a captive colony of zebra finches (Taeniopygia guttata). PLoS ONE 9:e89808 DOI 10.1371/journal.pone.0089808.

Birkhead TR, Burke T, Zann R, Hunter FM, Krupa AP. 1990. Extra-pair paternity and intraspecific brood parasitism in wild zebra finches Taeniopygia guttata. Revealed by DNA Fingerprinting 27:315–324.
Brazill-Boast J, van Rooij E, Pryke SR, Griffith SC. 2011. Interference from long-tailed finches constrains reproduction in the endangered Gouldian finch. *The Journal of Animal Ecology* **80**:39–48 DOI 10.1111/j.1365-2656.2010.01756.x.

Cleasby IR, Nakagawa S. 2012. The influence of male age on within-pair and extra-pair paternity in passerines. *Ibis* **154**:318–324 DOI 10.1111/j.1474-919X.2011.01209.x.

Cockburn A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B* **273**:1375–1383 DOI 10.1098/rspb.2005.3458.

Foerster K, Delhey K, Johnsen A, Lifjeld JT, Kempenaers B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* **425**:714–717 DOI 10.1038/nature01969.

Forstmeier W, Holger S, Schneider M, Kempenaers B. 2007. Development of polymorphic microsatellite markers for the zebra finch (*Taeniopygia guttata*). *Molecular Ecology Notes* **7**:1026–1028 DOI 10.1111/j.1471-8286.2007.01762.x.

Forstmeier W, Martin K, Bolund E, Schielzeth H, Kempenaers B. 2011. Female extrapair mating behavior can evolve via indirect selection on males. *Proceedings of the National Academy of Sciences of the United States of America* **108**:10608–10613 DOI 10.1073/pnas.1103195108.

Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B. 2014. Female extra-pair mating: adaptation or genetic constraint? *Trends in Ecology & Evolution* **29**:456–464 DOI 10.1016/j.tree.2014.05.005.

Griffith SC. 2007. The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. *The American Naturalist* **169**:282–283 DOI 10.1086/510606.

Griffith SC. 2010. The role of multiple mating and extra-pair paternity in creating and reinforcing boundaries between species in birds. *Emu* **110**:1–9 DOI 10.1071/MU09057.

Griffith SC, Holleley CE, Mariette MM, Pryke SR, Svedin N. 2010. Low level of extrapair parentage in wild zebra finches. *Animal Behaviour* **79**:261–264 DOI 10.1016/j.anbehav.2009.11.031.

Griffith SC, Immler S. 2009. Female infidelity and genetic compatibility in birds: the role of the genetically loaded raffle in understanding the function of extrapair paternity. *Journal of Avian Biology* **40**:97–101 DOI 10.1111/j.1600-048X.2009.04562.x.

Griffith SC, Stewart IANRK, Dawson DA, Owens IANPF, Burke T. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an “island effect”? *Biological Journal of the Linnean Society* **68**:303–316.

Griffith SC, Thuman KA, Owens IPF. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* **11**:2195–2212.

Higgins PJ, Peter JM, Cowling SJ. 2006. *Handbook of Australian, New Zealand and Antarctic birds. Boatbill to starlings*, vol. 7. Melbourne: Oxford University Press.

Jennings B, Edwards SV. 2005. Speciational history of Australian grass finches (*Poephila*) inferred from thirty gene trees. *Evolution* **59**:2033–2047.
Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**:1099–1106 DOI 10.1111/j.1365-294X.2007.03089.x.

Pryke SR, Rollins LA, Griffith SC. 2010. Females use multiple mating and genetically loaded sperm competition to target compatible genes. *Science* **329**:964–967 DOI 10.1126/science.1192407.

Rollins LA, Svedin N, Pryke SR, Griffith SC. 2012. The role of the Ord Arid Intrusion in the historical and contemporary genetic division of long-tailed finch subspecies in northern Australia. *Ecology and Evolution* **2**:1208–1219 DOI 10.1002/ece3.259.

Rowe M, Griffith SC, Hofgaard A, Lifjeld JT. 2015. Subspecific variation in sperm morphology and performance in the Long-tailed Finch (*Poephila acuticauda*). *Avian Research* **6**:23 DOI 10.1186/s40657-015-0032-z.

Sheldon BC. 1994. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proceedings of the Royal Society B* **257**:25–30 DOI 10.1098/rspb.1994.0089.

Van Rooij EP, Griffith SC. 2010. Are monomorphic species really sexually indistinguishable: no evidence in wild long-tailed finches (*Poephila acuticauda*). *Ethology* **116**:929–940 DOI 10.1111/j.1439-0310.2010.01808.x.

Van Rooij EP, Griffith SC. 2011. Breeding ecology of an Australian estrildid, the Long-tailed Finch (*Poephila acuticauda*). *Emu* **111**:297–303 DOI 10.1071/MU10092.

Van Rooij EP, Griffith SC. 2013. Synchronised provisioning at the nest: parental coordination over care in a socially monogamous species. *PeerJ* **1**:e232 DOI 10.7717/peerj.232.

Veen T, Borge T, Griffith SC, Saetre GP, Bures S, Gustafsson L, Sheldon BC. 2001. Hybridization and adaptive mate choice in flycatchers. *Nature* **411**:45–50 DOI 10.1038/35075000.

Whittingham LA, Dunn PO. 1999. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. *Behavioral Ecology* **16**:138–144.

Zann RA. 1996. *The Zebra Finch—a synthesis of field and laboratory studies*. Oxford: Oxford University Press.