

Intraspecific fledgling adoption by a pair of Superb Fairy-wrens *Malurus cyaneus*

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Abstract. Adoption is a form of alloparenting in which an individual raises an unrelated offspring, although it is sometimes unclear whether this behaviour is adaptive or the product of reproductive error. Here, we report an observation of intraspecific adoption in a cooperatively breeding songbird, the Superb Fairy-wren *Malurus cyaneus*. In a colour-banded population at Cleland Conservation Park, South Australia, a breeding pair with three nutritionally dependent fledglings adopted an additional male fledgling from an adjacent territory. The adoptee was first observed with the new group about 2 weeks after fledging and was regularly fed by his adoptive parents. The fledgling continued to associate with his adoptive group for at least 7 months, even though his natal group remained intact in the adjacent territory. Genetic analyses confirmed that the adopted fledgling was the product of within-pair mating and was not closely related to its adoptive parents. There is some evidence that adult fairy-wrens may discriminate against offspring based on the acoustic structure of their begging calls; however, begging calls recorded at the adoptee's nest were equally similar to incubation calls from both the genetic and adoptive mother. Finally, we discuss similar instances in the literature of intraspecific and interspecific adoption by Superb Fairy-wrens and suggest possible explanations for this behaviour.

Introduction

Alloparenting, in which individuals provide care to non-descendant offspring, has been documented in more than 150 bird species (Riedman 1982). Adoption is a rarer subset of alloparenting, and occurs when a foster parent raises an unrelated offspring as though it were its own (Riedman 1982; Avital *et al.* 1998). The reasons for adoption are sometimes unclear, given the apparent fitness costs for adoptive parents. In some cases, there may be no adaptive explanation: adoptive behaviour may occur as a result of reproductive error, when parents misidentify unrelated offspring as their own (Wysocki *et al.* 2018). However, several evolutionary explanations for adoptive behaviour have been proposed (Riedman 1982; Avital *et al.* 1998). If there is some degree of kinship between offspring and their adoptive parents, then adoption may improve the adoptive parents' inclusive fitness (Riedman 1982). Even when adopted offspring are unrelated, foster parents may gain parenting experience that enhances the fitness of their subsequent genetic offspring (Riedman 1982). In cooperatively breeding species, the 'group augmentation hypothesis' predicts that the costs of adopting an unrelated offspring may be outweighed by the benefits of gaining an additional group member (Kokko *et al.* 2002; Kingma *et al.* 2014).

Here, we report our observations of intraspecific adoptive behaviour by a breeding pair of Superb Fairy-wrens *Malurus cyaneus*, a cooperatively breeding passerine. A nutritionally dependent fledgling was adopted into a neighbouring territory and repeatedly fed by its adoptive parents. To explore possible explanations for this behaviour in an evolutionary context, we used genetic analyses to determine the fledgling's sex and genetic relatedness

to its adoptive parents. Because adult fairy-wrens may discriminate against offspring based on the acoustic structure of their begging calls (Colombelli-Négrel *et al.* 2012, 2016), we also assessed the vocal similarity between offspring begging calls and female incubation calls. We discuss similar instances in the literature of intraspecific and interspecific adoption by Superb Fairy-wrens and suggest possible explanations for this behaviour.

Methods

Study site and species

Since 2010, we have monitored a wild population of Superb Fairy-wrens at Cleland Wildlife Park (34°58'S, 138°41'E), located within Cleland Conservation Park, ~25 km east of Adelaide, South Australia. Superb Fairy-wrens are small passerines native to south-eastern Australia. They live in cooperatively breeding family groups, typically comprising a single breeding pair and one or more male helpers (Dunn *et al.* 1995). Both dominant and helper birds defend their territory against conspecific intruders (Rowley 1965). During the breeding season (September to January), females lay a clutch of 2–4 eggs and incubate for 14 days (Rowley & Russell 1997). Nestlings fledge at age 10–14 days, but do not become nutritionally independent until about 40 days old (Rowley & Russell 1997), by which time offspring also acquire their vocal repertoire from both parents (Evans & Kleindorfer 2016). All adult group members, including helper males, contribute to feeding offspring (Green *et al.* 1995). Superb Fairy-wrens have high rates of extra-pair paternity, with up to 76% of offspring unrelated to the dominant male in their natal territory (Mulder *et al.* 1994).

At our study site, most individuals (>90%) had been banded with an aluminium band (denoted by 'x') issued by the Australian Bird and Bat Banding Scheme (ABBBS), plus a unique combination of three plastic colour bands (ABBBS colour band schema 3) to allow identification in the field. The colour bands included dark blue (B), dark green (G), hot pink (H), black (N), orange (O), red (R), violet (V), white (W) and yellow (Y). Individuals were banded either as nestlings or, for fledglings and adults, after being captured in mist-nets. At the time of banding, we extracted 10–50- μ l blood samples from each bird by brachial venipuncture with a 30G needle. Each blood sample was collected into a heparinised capillary tube and stored on FTA® cards for later genetic analysis (Smith & Burgoyne 2004).

Monitoring of breeding season

Between September 2020 and February 2021, we monitored breeding in 27 fairy-wren territories at our study site. At each territory, we regularly searched for nests and watched the dominant female for nest-building or incubation behaviour. If a nest was discovered during building, then it was subsequently checked for egg-laying every 3 days. If discovered during incubation, then the eggs were candled to estimate the embryos' age. Around the expected hatch date, nests were checked at least once per day to confirm the nestlings' hatch date. At 8 days old, nestlings were banded and blood samples taken. We checked for fledging from 14 days after hatching.

On 6 November 2020, we identified two new Superb Fairy-wren territories (henceforth Groups 1 and 2), located 50–100 m outside our core study area. The habitat at these territories was stringybark *Eucalyptus* spp. woodland, with a complex understorey of small shrubs and grasses,

including Yacca *Xanthorrhoea semiplana semiplana* (Figure 1). Three of the four adults in these territories were colour-banded and had dispersed from the core study area within the past year. Group 1 comprised female NVHx (2+ years old) and an unbanded male (GBHx after 15 December 2020, age unknown), and Group 2 comprised female YGVx (2+ years old) and male RNHx (1 year old) (Figure 2).

Observations of feeding of fledglings

About 2 weeks after fledging, three observers (ACK, CE and LKC) observed each group for 60 minutes with binoculars and noted every time a fledgling was fed by an adult group member. For each feeding observation, we recorded the time when the feeding occurred (0–60 min. from the start of observation), the feeder (adult) and the food recipient (fledgling). Where possible, all fledglings in a group were observed simultaneously and without interruption; however, if the fledglings flew away from the observers, then the clock was paused until they were found again.

Comparison of calls

Female fairy-wrens produce an incubation call consisting of two main elements, known as Elements 'A' and 'B' (Colombelli-Négrel *et al.* 2012, 2016). While inside the egg, offspring are exposed to the calls of the incubating female and, after hatching, they produce begging calls that resemble the B element in their mother's calls (Colombelli-Négrel *et al.* 2012). Broods that more closely imitate their mother's call tend to receive more food, which suggests that parents may use the acoustic structure of begging calls to



Figure 1. Typical habitat in Superb Fairy-wren Group 1 and Group 2 territories, photographed in December 2020. Photo: Andrew C. Katsis



Figure 2. The adult breeding pair of Superb Fairy-wrens of Group 2, consisting of (a) male RNHx and (b) female YGVx. Photographed on 15 December 2020. Photos: Lauren K. Common

discriminate against ‘foreign’ offspring (Colombelli-Négrel *et al.* 2012, 2016). To test whether any such discrimination was likely in these two groups, we measured how closely begging calls from each nest resembled the incubation calls from the Group 1 and Group 2 breeding females. We followed a similar protocol to that used by Colombelli-Négrel *et al.* (2012). We recorded the females’ incubation calls on Day 12 of incubation (c. 2 days before hatching), by placing a digital audio recorder (Zoom H4n) 30 cm from the nest and allowing it to record for at least 180 minutes. Using the software Audacity (Audacity Team 2018), we randomly selected a single B element from 10 separate calls. Using the same methods, we recorded the offspring’s begging calls on Day 4 or 5 after hatching and selected 10 begging calls from two different calling bouts. We then compared the acoustic structure of female and offspring calls using the batch correlator function in Raven Pro v. 1.6.1 (K. Lisa Yang Center for Conservation Bioacoustics 2019). This function quantifies the similarity between two calls using spectrographic cross-correlation, which slides two spectrograms past each other in time increments and then generates a peak correlation coefficient to represent their greatest overlap (Baker & Logue 2003). Correlation coefficients can range between 0 (not similar) and 1 (identical). Our SPCC analyses used a band-pass filter between 2 and 16 kHz to exclude background noise. We performed 100 comparisons per brood (10 begging calls \times 10 incubation calls) before calculating the mean peak correlation coefficient. These comparisons were performed at the brood (rather than individual) level, as we could not distinguish between begging calls from different nestlings calling in the nest. In a larger study of Superb Fairy-wrens, the mean \pm standard error similarity between nestling begging calls and their mother’s element B was 0.56 ± 0.02 (range 0.24–0.68, $n = 30$ nests) (Kleindorfer *et al.* unpubl. data).

Genetic analyses

We commissioned genetic analyses to establish the sex and paternity of the adopted fledgling. Sex was confirmed with established molecular techniques, using three primer pairs for which males are homogametic and females heterogametic (CHD1F/CHD1R, P2/P8 and 2550F/2718R: Griffiths *et al.* 1998; Fridolfsson & Ellegren 1999; Lee *et al.* 2010). To establish relatedness between individuals, all birds in our study population ($n = 193$) were genotyped at 12 polymorphic microsatellite loci using primers developed for the Superb Fairy-wren (Mcyu1, Mcyu4, Mcyu5, Mcyu6, Mcy7, Mcy8: Double *et al.* 1997), Splendid Fairy-wren *Malurus splendens* (Msp4, Msp6, Msp10: Webster *et al.* 2004), Southern Emu-wren *Stipiturus malachurus* (Smm2, Smm7: Maguire *et al.* 2006) and Malagasy Paradise Flycatcher *Terpsiphone mutata* (Tmm6: Adcock & Mulder 2002). We calculated maximum likelihood estimates of relatedness (R) for all pairwise combinations within the population, using the software ML-Relate (Kalinowski *et al.* 2006). Two loci (Mcy7, Mcyu5) had significant departure from Hardy–Weinberg equilibrium and were specified as null alleles; this allowed the software to use maximum likelihood estimates of the frequency of null alleles in all calculations (as per Kalinowski & Taper 2006). We theoretically expect relatedness values of 0.5 for parent–offspring and full-sibling comparisons, 0.25 for half-siblings and grandparent–grandchild, 0.125 for first cousins, and 0.0 when comparing two unrelated individuals, although inbreeding and migration can bias these estimates (Kalinowski *et al.* 2006). DNA extraction and genetic analyses were performed commercially by the Australian Genome Research Facility (Melbourne, Australia).



Figure 3. The adopted fledgling Superb Fairy-wren, GOOx, at three stages of development: (a) 1-day-old hatchling in Group 1 nest, 18 November 2020; (b) 8-day-old nestling in Group 1 nest, 25 November 2020; and (c) 28-day-old fledgling when captured with Group 2, 15 December 2020. Photos: (a) Christine Evans, (b) Andrew C. Katsis, and (c) Lauren K. Common

Results

Behavioural observations

On 6 November 2020, we discovered a nest belonging to Group 1. It contained three eggs, estimated as 2–3 days old. Two chicks hatched on 18 November and, at 8 days old, they were banded as GOOx and YVBx, respectively. Also on 6 November 2020, we discovered an empty nest belonging to Group 2, located about 50 m from the Group 1 nest. Female YGVx started incubating three eggs on 10 November. Three chicks hatched on 23 November and were banded as YNBx, HVWx and ROOx, respectively, at 8 days old.

We expected the Group 1 offspring to fledge around 1 December and the Group 2 offspring to fledge around 5 December. On 6 December, we sought to confirm fledging at both territories. In Group 1, we identified only one surviving fledgling: YVBx was encountered four times over a 20-minute period, and we did not observe its sibling, GOOx, at all. In Group 2, we confirmed all three fledglings over a 20-minute period. Because we stopped observing immediately after confirming these three fledglings, it is possible that additional birds in this group went unnoticed.

On 14 December, over a 60-minute period we observed feeding of fledglings in Group 2. We observed the Group 2 parents regularly feeding four fledglings: their three genetic offspring (YNBx, HVWx, ROOx) plus GOOx from Group 1 (photograph in Figure 3). The adopted fledgling, GOOx, was fed eight times during this 60-minute observation period, receiving the second-most feedings among the four dependent fledglings (Table 1). We did not observe Group 1 in its usual territory, despite a 15-minute search of the area; however, the following day we confirmed that the group was still extant, with all other group members alive. On 17 December, we conducted a 60-minute observation of fledgling feeding in Group 1. The male and female of

the breeding pair were observed feeding their remaining fledgling, YVBx, and GOOx was not observed with its natal group.

Over the next 5 weeks, GOOx was observed with Group 2 on six separate occasions (15, 17 and 23 December, and 5, 14 and 20 January). On these dates, Group 1 was either not observed or was located at least 50 m away, confirming that both groups were foraging independently. GOOx remained with Group 2 for at least 7 months (last sighted 30 July 2021).

Call comparisons

Begging calls from both broods were comparably similar to the incubation calls from each breeding female. Compared with the Group 1 female (NVHx), mean call similarity was 0.248 for the Group 1 brood and 0.241 for the Group 2 brood. Compared with the Group 2 female (YGVx), mean call similarity was 0.135 for the Group 1 brood and 0.154 for the Group 2 brood. Similarity values at both nests were lower than we have typically measured in Superb Fairy-wrens (e.g. call similarity ranged from 0.24 to 0.68: Kleindorfer *et al.* unpubl. data).

Genetic analyses

Molecular sexing confirmed that the adopted fledgling, GOOx, was male. Taking his biological mother's (NVHx) alleles into account, GOOx matched the Group 1 male (GBHx) at all 12 microsatellite loci, consistent with within-pair paternity. The adopted fledgling's maximum likelihood estimates of relatedness (R) were 0.53 compared with NVHx and 0.65 compared with GBHx. These values are comparable to the theoretically expected R of 0.5 for parent-offspring relationships (Kalinowski *et al.* 2006).

Table 1. Data on feeding of Superb Fairy-wren fledglings from 60-minute observations of Group 1 (17 December) and Group 2 (14 December 2020). For each observation, we noted the minute (0–60, from start of observations) when the feeding occurred, the feeder (adult) and the recipient (fledgling). The fledgling GOOx originated from Group 1 but was adopted into Group 2 while still nutritionally dependent. F = female, M = male. See text for details of banded birds. † = Recipient ambiguous; assigned to fledgling YNBx but could have been HVWx. * = Feeding not directly observed but inferred from the birds' positions and vocalisations.

Feeder		Recipient		
Group 1				
	YVBx	GOOx		
NVHx, F	1, 8, 19, 19, 47, 55	Not seen		
GBHx, M	9, 31, 41, 59	Not seen		
Total no. feeds	10	0		
Group 2				
	YNBx	HVWx	ROOx	GOOx
YGVx, F	14, 15, 24, 38†, 49	20, 39*, 47, 48	5*, 9, 25, 31, 32*, 36, 40, 45, 54, 57, 59	6, 11*, 18, 24
RNHx, M	37†	27	21, 55	7, 49, 52, 53
Total no. feeds	6	5	13	8

Conversely, GOOx matched the Group 2 male (RNHx) at only three microsatellite loci and was not related to either member of the pair ($R = 0.00$ compared with both Group 2 adults).

Discussion

In wild bird populations, fledgling adoption can be difficult to confirm when individuals are not uniquely identifiable. Our observations provide unequivocal evidence for adoptive behaviour in the Superb Fairy-wren, as the adopted offspring (GOOx) was banded in the nest and we are certain of its age and provenance. Despite being a widely studied species, intraspecific adoption has only rarely been observed in Superb Fairy-wrens, and when it occurs is often associated with the loss of a breeding male or female. For example, Rowley (1957, p. 356) described one helper male at Gungahlin, Australian Capital Territory, that dispersed into a neighbouring group and adopted that group's extant offspring:

At one nest the male parent disappeared (presumed dead) when the young were still in the nest. A supernumerary male from the neighbouring group joined the female and fed the young, and when she also disappeared he remained with his adopted fledglings and reared them to independence.

Similarly, Richardson *et al.* (2019) reported a case of adoption by a female Superb Fairy-wren at Lake Samsonvale, Queensland: the female was observed feeding fledglings from a nearby territory 10 days after losing her own brood to predation. They suggested that the most likely explanation for this behaviour was that the female's parenting impulse persisted after the loss of her own brood and was redirected towards unrelated offspring. Our observation differs from these accounts in that both of our fairy-wren groups (Groups 1 and 2) were fully intact at the time of the adoption, and hence warrants its own explanation.

We propose two possible reasons why GOOx joined a new group so soon after fledging. Firstly, the adoption could be interpreted as an unusually early offspring dispersal. Superb Fairy-wren fledglings are shy and cryptic in their first week after leaving the nest; they keep closely to cover, are weak and erratic flyers, and wholly rely on their family members for food (Rowley 1965; our pers. obs.). After this period, the fledglings venture into the open and may begin to forage themselves, but remain nutritionally dependent until c. 3–4 weeks post-fledging (Rowley 1965; Rowley & Russell 1997). The first wave of female dispersal generally does not occur until 5–14 weeks post-fledging, seemingly at the offspring's own volition (Mulder 1995). By comparison, GOOx would have dispersed no more than 2 weeks out of the nest, while still heavily dependent on adults for food. Mulder (1995) mentioned one female that also changed groups only 2 weeks after fledging, presumably while still nutritionally dependent, but did not report whether she was fed in her new territory. In any case, we consider deliberate dispersal to be an unlikely explanation for our observations, not only because GOOx was still dependent on adult food provisioning when he switched groups, but also because he was male. Although a small proportion of male offspring disperse to a new territory in their first year (13% in Mulder 1995), most remain in their natal territory for longer.

Secondly, the fledgling might have been separated from his natal group and joined Group 2 by mistake. Groups 1 and 2 occupied adjacent territories and, on at least one occasion, were observed engaging in a defensive 'song battle' (Rowley 1965) at their territories' shared boundary. It is plausible that an inexperienced fledgling might follow the wrong group after such a close interaction, especially if that group also contained begging fledglings. Rowley (1965, p. 280) recounted a similar confusion that occurred between two neighbouring groups at Gungahlin:

Parents seem unable to identify their own offspring in the early days after fledging, as was shown when two neighbouring nests hatched simultaneously and the cryptic young from both became completely and

hopelessly mixed up. Territorial barriers disintegrated and all parents (plus a previously “bachelor” male from a third territory) fed the fledglings indiscriminately. After about a week one pair withdrew to their former territory and re-nested, leaving the other pair plus the bachelor to care for all six fledglings, which they did successfully. Such a coincidence of timing rarely occurs and the formation of such a crèche was not seen again.

In contrast with this account, in our study the two fairy-wren groups apparently remained separate throughout the observation period. However, we cannot exclude the possibility that the two groups fraternised before the observed adoption (i.e. between our observations on 6 and 14 December). We also note that the Group 1 female re-nested about a week after the adoption was discovered, with her new brood of three offspring hatching on 7 January 2021.

The reasons for the fledgling's acceptance into Group 2 are also unclear. The simplest explanation, as suggested by Rowley (1965) above, is that the Group 2 pair was unable to recognise its own kin and simply fed any offspring that solicited food. Such misidentifications are plausible in fairy-wrens, given their high susceptibility to interspecific brood-parasitism (Langmore *et al.* 2003). However, we also have evidence that fairy-wrens may discriminate between offspring based on their begging calls (Colombelli-Négrel *et al.* 2012, 2016). The structure of nestling begging calls is influenced by the prenatal sound environment, with offspring shaping their calls to match a signature element in their mother's incubation call (Colombelli-Négrel *et al.* 2012). This prenatal learning may allow parents to discriminate between kin and non-kin: in a playback experiment, they were less likely to provision their nestlings when begging calls from a different brood were broadcast at the nest (Colombelli-Négrel *et al.* 2012). Recognition errors may nevertheless occur, not least because offspring vary in their level of copy accuracy of the maternal signature element (Kleindorfer *et al.* 2014). In our analyses, begging calls from both broods were comparably similar to the adoptive female's Element B (mean peak similarity: 0.135 for the Group 1 brood, 0.154 for the Group 2 brood), which suggests little scope for kin discrimination based on begging calls alone. However, we note that begging calls were recorded when offspring were aged 4–5 days, c. 3 weeks before the adoption was confirmed to occur. To date, no studies on Superb Fairy-wrens have examined how begging call structure changes between the nestling and fledgling stages. In addition, future research could address to what degree parents use acquired vocal elements to recognise offspring, given that fledglings produce a ‘familect’ song composed of unique and shared elements in their mother's and father's chatter song (Evans & Kleindorfer 2016).

In addition to the intraspecific adoptions described here, there is at least one published account of a Superb Fairy-wren adopting heterospecific offspring. Cooper (1969) observed a male Superb Fairy-wren feeding a Red-backed Fairy-wren *Malurus melanocephalus* fledgling, alongside the fledgling's conspecific parents, at Grafton, New South Wales. Richardson *et al.* (2019) cited an additional instance of interspecific adoption observed by S.C. Tidemann at Booligal, New South Wales, but the motivations of the adoptive parent are ambiguous. As originally reported by Tidemann (1983), the dominant male

in a Superb Fairy-wren group died, leaving behind two females that continued to feed the offspring in their care: a brood-parasitic Horsfield's Bronze-Cuckoo *Chalcites basalis*. A neighbouring male then brought food to one of the attending females, which passed it onto the Cuckoo (Tidemann 1983). Based on this account, it is not clear that the neighbouring male had adopted the Cuckoo rather than simply presented food to a potential mate. However, this observation was later recounted by Higgins *et al.* (2001) with several erroneous details, changing the sex of the adoptive parent and implying that the Cuckoo was fed directly.

One explanation for the success of brood-parasites is that heterospecific offspring elicit more parental care from their hosts by producing supernormal stimuli, which are exaggerated versions of sensory signals (e.g. begging calls, gape colour) to which parents have an existing evolved response (the ‘supernormal stimulus hypothesis’: Dawkins & Krebs 1979; Grim & Honza 2001). In our study, the adopted Group 1 fledgling, although conspecific, was 5 days older than the Group 2 fledglings, which might have allowed him to beg more loudly or persistently than the others, potentially producing a supernormal stimulus. We did not measure begging frequency during our 60-minute observation periods; however, we did note qualitatively that, among the four fledglings, ROOx and GOOx followed the Group 2 parents most closely and begged more frequently. Accordingly, they also received the most feedings.

Even if the fledgling were recognised by its adoptive parents as non-kin, there may be benefits to accepting unrelated offspring into the group – especially in cooperatively breeding species, where additional helpers can enhance the fitness of the entire group (Kokko *et al.* 2002; Kingma *et al.* 2014; Langmore *et al.* 2016). In the White-winged Chough *Corcorax melanorhamphos*, for example, kidnapped fledglings from neighbouring groups later continue as helpers in their adoptive group. In these cases, the initial costs of supporting an unrelated fledgling may be outweighed by the benefits of an additional helper (Heinsohn 1991). Superb Fairy-wrens are also cooperative breeders, with male offspring often remaining as helpers in their natal territory for ≥ 1 year (Rowley & Russell 1997). These helpers assist with provisioning of offspring, and this provides increased opportunities for extra-pair mating for both members of the breeding pair (Mulder *et al.* 1994; Green *et al.* 1995). Hence, Superb Fairy-wrens may tolerate an unrelated male fledgling because of the benefits of gaining an additional group member.

In this note, we describe an observation of intraspecific adoption by a breeding pair of Superb Fairy-wrens. Adoptive behaviour has only rarely been documented in this species; however, such behaviour could go unnoticed in many cases if offspring are not uniquely marked in the nest and/or regularly monitored. Although adoption of unrelated offspring may have an adaptive function in some birds, including in cooperatively breeding species, this instance may simply be a case of reproductive error.

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References

- Adcock, G.J. & Mulder, R.A. (2002). Polymorphic microsatellite loci for paternity analysis in the Madagascar paradise flycatcher (*Terpsiphone mutata*: Aves). *Molecular Ecology Notes* **2**, 287–289.
- Audacity Team (2018). *Audacity: Free Audio Editor and Recorder*. Version 2.3.2.
- Avital, E., Jablonka, E. & Lachmann, M. (1998). Adopting adoption. *Animal Behaviour* **55**, 1451–1459.
- Baker, M.C. & Logue, D.M. (2003). Population differentiation in a complex bird sound: A comparison of three bioacoustical analysis procedures. *Ethology* **109**, 223–242.
- Colombelli-Négrel, D., Hauber, M.E., Robertson, J., Sulloway, F.J., Hoi, H., Griggio, M. & Kleindorfer, S. (2012). Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. *Current Biology* **22**, 2155–2160.
- Colombelli-Négrel, D., Webster, M.S., Dowling, J.L., Hauber, M.E. & Kleindorfer, S. (2016). Vocal imitation of mother's calls by begging Red-backed Fairy-wren nestlings increases parental provisioning. *Auk* **133**, 273–285.
- Cooper, R.P. (1969). Multiple feeding habits of wrens. *Australian Bird Watcher* **3**, 145–150.
- Dawkins, R. & Krebs, J.R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **205**, 489–511.
- Double, M.C., Dawson, D., Burke, T. & Cockburn, A. (1997). Finding the fathers in the least faithful bird: A microsatellite-based genotyping system for the superb fairy-wren *Malurus cyaneus*. *Molecular Ecology* **6**, 691–693.
- Dunn, P.O., Cockburn, A. & Mulder, R.A. (1995). Fairy-wren helpers often care for young to which they are unrelated. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **259**, 339–343.
- Evans, C. & Kleindorfer, S. (2016). Superb fairy-wren (*Malurus cyaneus*) sons and daughters acquire song elements of mothers and social fathers. *Frontiers in Ecology and Evolution* **4**, 9.
- Fridolfsson, A.-K. & Ellegren, H. (1999). A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**, 116–121.
- Green, D.J., Cockburn, A., Hall, M.L., Osmond, H. & Dunn, P.O. (1995). Increased opportunities for cuckoldry may be why dominant male fairy-wrens tolerate helpers. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **262**, 297–303.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998). A DNA test to sex most birds. *Molecular Ecology* **7**, 1071–1075.
- Grim, T. & Honza, M. (2001). Does supernormal stimulus influence parental behaviour of the cuckoo's host? *Behavioral Ecology and Sociobiology* **49**, 322–329.
- Heinsohn, R.G. (1991). Kidnapping and reciprocity in cooperatively breeding white-winged choughs. *Animal Behaviour* **41**, 1097–1100.
- Higgins, P.J., Peter, J.M. & Steele, W.K. (Eds) (2001). *Handbook of Australian, New Zealand & Antarctic Birds, Volume 5: Tyrant Flycatchers to Chats*. Oxford University Press, Melbourne.
- K. Lisa Yang Center for Conservation Bioacoustics (2019). *Raven Pro: Interactive Sound Analysis Software*. Version 1.6.1. Cornell Lab of Ornithology. <http://ravensoundsoftware.com/>
- Kalinowski, S.T. & Taper, M.L. (2006). Maximum likelihood estimation of the frequency of null alleles at microsatellite loci. *Conservation Genetics* **7**, 991–995.
- Kalinowski, S.T., Wagner, A.P. & Taper, M.L. (2006). ML-Relate: A computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes* **6**, 576–579.
- Kingma, S.A., Santema, P., Taborsky, M. & Komdeur, J. (2014). Group augmentation and the evolution of cooperation. *Trends in Ecology & Evolution* **29**, 476–484.
- Kleindorfer, S., Evans, C. & Colombelli-Négrel, D. (2014). Females that experience threat are better teachers. *Biology Letters* **10**, 20140046.
- Kokko, H., Johnstone, R.A. & Wright, J. (2002). The evolution of parental and alloparental effort in cooperatively breeding groups: When should helpers pay to stay? *Behavioral Ecology* **13**, 291–300.
- Langmore, N.E., Bailey, L.D., Heinsohn, R.G., Russell, A.F. & Kilner, R.M. (2016). Egg size investment in superb fairy-wrens: Helper effects are modulated by climate. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20161875.
- Langmore, N.E., Hunt, S. & Kilner, R.M. (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**, 157–160.
- Lee, J.C.-I., Tsai, L.-C., Hwa, P.-Y., Chan, C.-L., Huang, A., Chin, S.-C., Wang, L.-C., Lin, J.-T., Linacre, A. & Hsieh, H.-M. (2010). A novel strategy for avian species and gender identification using the CHD gene. *Molecular and Cellular Probes* **24**, 27–31.
- Maguire, G.S., Guay, P.-J. & Mulder, R.A. (2006). Isolation and characterization of microsatellite markers in the southern emu-wren (*Stipiturus malachurus*: Aves). *Molecular Ecology Notes* **6**, 422–424.
- Mulder, R.A. (1995). Natal and breeding dispersal in a cooperative, extra-group-mating bird. *Journal of Avian Biology* **26**, 234–240.
- Mulder, R.A., Dunn, P.O., Cockburn, A., Lazenby-Cohen, K.A. & Howell, M.J. (1994). Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **255**, 223–229.
- Richardson, N.M., Kennerley, J.A. & Feeney, W.E. (2019). First record of intraspecific adoption by a female Superb Fairy-wren *Malurus cyaneus*. *Sunbird* **48**, 159–161.
- Riedman, M.L. (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology* **57**, 405–435.
- Rowley, I. (1957). Co-operative feeding of young by Superb Blue Wrens. *Emu* **57**, 356–357.
- Rowley, I. (1965). The life history of the Superb Blue Wren, *Malurus cyaneus*. *Emu* **64**, 251–297.
- Rowley, I. & Russell, E. (1997). *Fairy-wrens and Grasswrens: Maluridae*. Oxford University Press, Oxford, UK.
- Smith, L.M. & Burgoyne, L.A. (2004). Collecting, archiving and processing DNA from wildlife samples using FTA® databasing paper. *BMC Ecology* **4**, 4.
- Tidemann, S.C. (1983). The Behavioural Ecology of Three Coexisting Fairy-wrens (Maluridae: *Malurus*). PhD thesis. Australian National University, Canberra.
- Webster, M.S., Tarvin, K.A., Tuttle, E.M. & Pruett-Jones, S. (2004). Reproductive promiscuity in the splendid fairy-wren: Effects of group size and auxiliary reproduction. *Behavioral Ecology* **15**, 907–915.
- Wysocki, D., Cholewa, M. & Jankowiak, Ł. (2018). Fledgling adoption in European Blackbirds: An unrecognized phenomenon in a well-known species. *Behavioral Ecology* **29**, 230–235.