Escalation of a coevolutionary arms race through host rejection of brood parasitic young

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indicate that core formation occurred in planetesimals within about 3 Myr (refs 1, 2) of Solar System formation. If the lowest initial ratios are used for both radionuclides, the temperature would not reach the Fe-FeS melting point and core segregation could not occur in the absence of another heat source (Fig. 2a). However, in general the heat provided by radioactive decay is sufficient to heat a planetesimal to the Fe-FeS melting point, resulting in metal segregation within the timeframe allowed by W isotopes. If high initial ratios are used for both radionuclides then the silicate melting point could be reached as well, and any trapped Fe alloy remaining after initial segregation would also segregate. Another consequence of a high initial $^{60}Fe/^{56}Fe$ is considerable heating in the core of the planet after metal segregation. The amount of superheat produced can be prodigious, and is a plausible heat source for early volcanism on planetesimals and internal differentiation as indicated by ordinary chondrite meteorites[20].

Our results indicate that planetesimals with radii greater than about 30 km and larger planetary embryos are expected to have formed cores very early, and these objects would have contained much of the mass in the terrestrial region of the protoplanetary nebula[22]. The Earth and other terrestrial planets are likely to have formed by accretion of previously differentiated planetesimals, and Earth's core may be viewed as a blended composite of pre-formed cores. □

Methods

Materials and experimental techniques

San Carlos olivine was mixed with reagent-grade FeS in volume ratios of 100:0, 97:3, 94:6 and 87:13, and with $Fe_{64}S_{36}$ in volume ratios of 100:0, 97:3, 94:6 and 88:12. The mixtures were finely ground and most grains were 5–10 μm in diameter, with occasional larger grains (10–100 μm). The sample was packed into a boron nitride (BN) capsule, and was 1 mm in diameter and 3 mm long. The BN capsule was surrounded by molybdenum foil so that the oxygen fugacity would be close to the $Mo-MoO_2$ buffer, and was placed at the centre of a graphite heating element. Graphite electrodes were placed in contact with the sample, and measured resistance included the electrodes in addition to the sample. A reference resistance (10^2 or $10^3 \Omega$) was connected to the sample in series, and a sinusoidal signal with an amplitude of 1 V and a frequency in the range 0.1–0.01 Hz was applied to the circuit. Voltages on the sample and reference were measured simultaneously. The sample resistance was calculated from that of the reference and the ratio of voltage on the sample to that on the reference. Sample conductivity was calculated from the resistance and the sample dimensions. We measured the electrical conductivity of polycrystalline olivine without Fe-S compounds to establish a reference for the experimental configuration. The conductivity of the reference was very low ($\sim 10^{-3} S\,m^{-1}$) up to nearly 700 °C, and then rapidly increased with temperature to 1,300 °C (9 S m^{-1}). The electrical conductivity from 700 to 1,300 °C is not attributed to olivine, which has a much lower conductivity at 1,300 °C ($3 \times 10^{-3} S\,m^{-1}$)[23], but to the BN capsule. The temperature–conductivity path for this reference established a baseline below which values are not derived from the sample.

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Escalation of a coevolutionary arms race through host rejection of brood parasitic young

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Cuckoo nestlings that evict all other young from the nest soon after hatching impose a high reproductive cost on their hosts[1]. In defence, hosts have coevolved strategies to prevent brood parasitism. Puzzlingly, they do not extend beyond the egg stage[2–5]. Thus, hosts adept at recognizing foreign eggs remain vulnerable to exploitation by cuckoo nestlings[6,7]. Here we show that the breach of host egg defences by cuckoos creates a new stage in the coevolutionary cycle. We found that defences used during the egg-laying period by host superb fairy-wrens (*Malurus cyaneus*) are easily evaded by the Horsfield's bronze-cuckoo (*Chrysococcyx basalis*), a specialist fairy-wren brood parasite. However, although hosts never deserted their own broods, they later abandoned 40% of nests containing a lone Horsfield's bronze-cuckoo nestling, and 100% of nests with a lone shining bronze-cuckoo nestling (*Chrysococcyx lucidus*), an occasional fairy-wren brood parasite. Our experiments demonstrate that host discrimination against evictor-cuckoo nestlings is possible, and suggest that it has selected for the evolution of nestling mimicry in bronze-cuckoos.

The Horsfield's bronze-cuckoo is an Australian brood parasite that lays a white egg covered with fine red-brown speckling, closely resembling the eggs of its fairy-wren (Maluridae) and thornbill (Acanthizidae) hosts (Fig. 1a). Within 48 h of hatching, the cuckoo

nestling evicts host eggs or young[8] and so becomes the sole occupant of the nest. At our study site in Campbell Park, Canberra, Australia, 19–37% of superb fairy-wren nests per year contained an egg of the Horsfield's bronze-cuckoo (1999–2002, $N = 349$ nests in which eggs were laid). The fairy-wren's response depended on the timing of parasitism. Cuckoo eggs laid before the host commenced laying were usually sewn into the nest lining (13 out of 15), ensuring that they would fail to hatch, whereas those laid during the host-laying period were almost all accepted (52 out of 53; before versus during comparison, G-statistic test, $G^2 = 47.5$, $P < 0.0001$). When the cuckoo added her egg after the host had begun incubation, the clutch was usually deserted (7 out of 8; during versus after comparison $G^2 = 31.5$, $P < 0.0001$), but when we placed cuckoo eggs in the nest after incubation had begun they were accepted (26 out of 27, natural parasitism versus relocated eggs, $G^2 = 23.1$, $P < 0.0001$). Desertion was therefore triggered by the presence of an adult female cuckoo that was more likely to be caught at the nest by hosts during incubation than during egg laying. The presence of the cuckoo egg itself did not provoke desertion. The effective parasitism rate (excluding buried or deserted cuckoo eggs) ranged from 16–32% per year.

In further experiments, we tested whether fairy-wrens ever discriminated against foreign eggs. During the egg-laying period, we added to the nest a painted egg that differed from the fairy-wren's in colour, pattern or size (see Methods). Fairy-wrens did not reject odd eggs on the basis of colour or pattern (3 out of 16 blue, 2 out of 11 spotted, 4 out of 18 fairy-wren colour, 0 out of 7 brown painted real eggs deserted or rejected; $\chi^2 = 1.8$, 3 degrees of freedom (d.f.), $P = 0.62$; see also ref. 8), but they were more likely to desert clutches containing an egg larger than their own (7 out of 15 big versus 1 out

of 11 small parchment-coloured model eggs deserted or rejected; $G^2 = 4.2$, $P = 0.04$). The dim interior of the fairy-wren's domed nest (mean plus standard error = $976 + 105$ lx, $N = 107$ nests) may have promoted tactile, rather than visual recognition of foreign eggs, a strategy seen in other dome-nesting host species[5,9]. However, it is a poor defence against the Horsfield's bronze-cuckoo, which lays a relatively small egg[10], similar in size to fairy-wren eggs (Fig. 1b). In summary, our data show that fairy-wrens can mount some defences against parasitism around the time of egg laying but they do not reject or desert foreign eggs by their appearance. Providing that the Horsfield's bronze-cuckoo female times her egg laying to coincide with that of her targeted host, she will beat host defences at this stage of the nesting cycle.

Acceptance of cuckoo eggs can result in a stable end to the arms race[11–13] but if parasitism rates are consistently high, hosts would benefit from the evolution of new defences against cuckoo parasitism. The coevolutionary arms race between superb fairy-wrens and Horsfield's bronze-cuckoos has escalated to the stage of discrimination against cuckoo chicks. Through observations at unmanipulated nests, we found that superb fairy-wrens deserted 11 out of 29 (11 out of 42 including depredated nests) Horsfield's bronze-cuckoo nestlings (see also ref. 14) but they never abandoned broods of their own young ($N = 95$ nests, 18 with daily nest watches). The likelihood of cuckoo chick desertion was not influenced by whether any host young had hatched before eviction ($N = 37$, $G^2 = 0.83$, 1 d.f., $P = 0.36$), nor was there a time-of-season effect (desertion rate against month September to January, $G^2 = 1.9$, 4 d.f., $P = 0.7$). In all 11 cases of desertion, and usually when the cuckoo was 3–6 days old ($N = 7$), the female stopped provisioning the cuckoo and, while it was still alive, began building a new nest and soliciting copulations. Although the male(s) in the group sometimes continued feeding the cuckoo for up to three days longer (5 cases), it eventually died from cold or starvation. The corpse was then typically devoured by meat ants *Iridomyrmex purpureus*. Although previous studies of other brood parasitic species have found that some non-evicting parasitic chicks are less effective at eliciting care from their foster parents than host nestlings[15–17], ours shows unambiguously that hosts can reject alien young in their nest.

To test how fairy-wren females recognized a cuckoo in their nest,
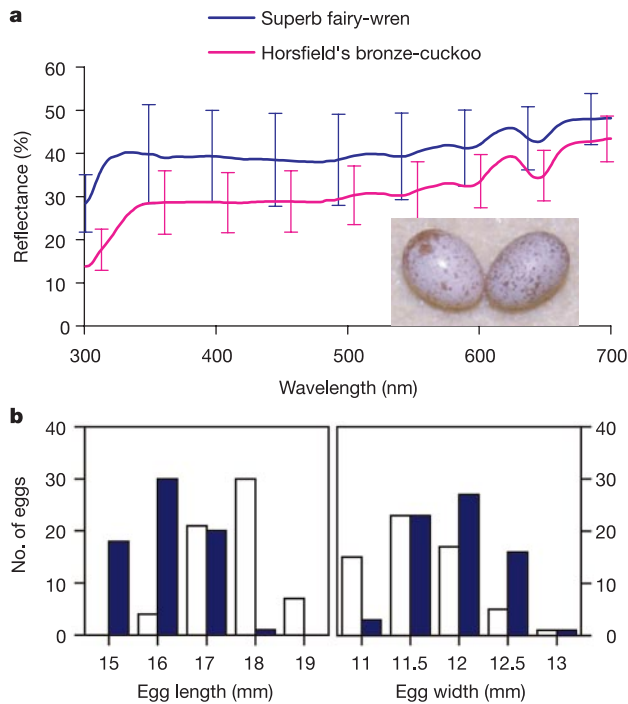
Figure 1 Comparisons of Horsfield's bronze-cuckoo and fairy-wren eggs. **a**, Mean ($\pm$s.d.) spectral reflectance of Horsfield's bronze-cuckoo eggs (pink line, $N = 9$) and superb fairy-wren eggs (blue line, $N = 26$ from 16 clutches). Standard deviations represent variation within and between eggs. There was a close colour match between cuckoo and host eggs. Cuckoo eggs were slightly less reflective (principal components analysis[27], 9 eggs per species, PC1: $F_{1,16} = 7.80$, $P = 0.013$), probably because they have more dark speckling at the narrower end. The photograph shows a superb fairy-wren egg (left) and a Horsfield's bronze-cuckoo egg (right). **b**, Distribution of egg length and width for Horsfield's bronze-cuckoos (white bars) and superb fairy-wrens (blue bars).
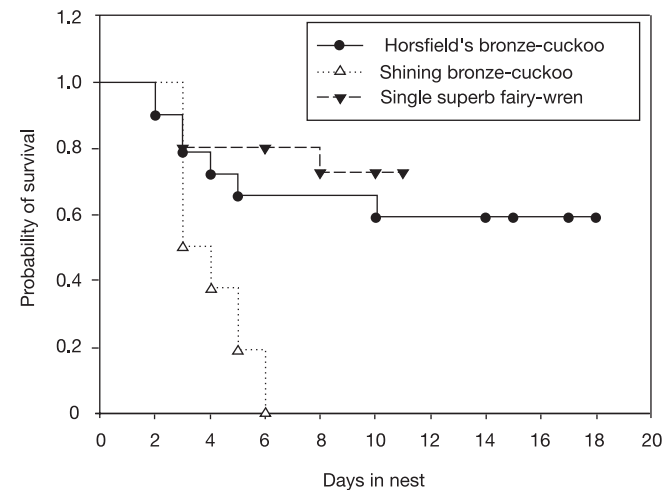
Figure 2 Kaplan–Meier estimate of the survival functions of Horsfield's bronze-cuckoo chicks, shining bronze-cuckoo chicks and lone superb fairy-wren chicks in superb fairy-wren nests. The probability of survival differed significantly between the three species ($\chi^2 = 9.01$, 2 d.f., $P = 0.01$). Comparing probability of survival to that of a single fairy-wren, there was no difference in the risk ratio for Horsfield's bronze-cuckoos (risk ratio = 0.82, 95% confidence limits 0.4, 1.59), whereas there was a significant difference for shining bronze-cuckoos (risk ratio = 2.44, 95% confidence limits 1.21, 4.85).

we manipulated clutches (see Methods) so that after hatching, nests contained either a lone Horsfield's bronze-cuckoo chick ($N = 20$), a lone shining bronze-cuckoo chick ($N = 8$), or a lone fairy-wren chick ($N = 14$). Desertion occurred in all three treatments, which suggests that, in part, females recognize cuckoos simply because they are alone in the nest. However, other cues must be important because shining bronze-cuckoo chicks were always abandoned, whereas single fairy-wren chicks and Horsfield's bronze-cuckoos were deserted at a significantly lower and similar rate (Fig. 2).

We suggest that chick desertion by hosts has evolved in response to cuckoo parasitism. Our experiment shows that cuckoo chick desertion is not simply a by-product of a life history strategy to avoid wasting time on single chick broods. If broods containing a single chick were unprofitable, abandonment of lone chicks should have occurred with equal frequency for all three species. Nor is the consistent desertion of any lone chick a strategy practised by a subset of the female population. Ten females were parasitized by lone chicks of two species; two out of five that reared a lone fairy-wren chick subsequently deserted a Horsfield's bronze-cuckoo chick, and five out of five reared a Horsfield's bronze-cuckoo chick but deserted a shining bronze-cuckoo chick. Furthermore, chick desertion cannot be a pre-existing strategy against non-kin in the nest because host females take the decision to abandon the cuckoo even though they are always related to their entire brood at unparasitized nests ($N = 40$ broods[18]), whereas males commonly are not[18].

As the rare fairy-wren parasite (shining bronze-cuckoo) was routinely recognized by hosts, whereas the specialist parasite (Horsfield's bronze-cuckoo) was less frequently abandoned, host defences

against cuckoo chicks appear to have caused reciprocal adaptations in cuckoo nestlings. Preliminary experimental evidence suggests that hosts do not use visual cues to distinguish cuckoo chicks. Shining bronze-cuckoo chicks hatch in one of two distinct colour morphs: a pinkish-yellow morph, which appears similar to fairy-wren chicks (Fig. 3b), or a black morph (Fig. 3c), which differs markedly from host young. Horsfield's bronze-cuckoos chicks are intermediate in colour (Fig. 3a). Despite their similarity to host young, pale morph shining bronze-cuckoo chicks were always deserted by hosts ($N = 4$), whereas the more alien looking Horsfield's bronze-cuckoo chicks were often accepted (14 out of 20; Fisher's exact test, $P = 0.02$).

We suggest that discrimination of vocal cues by hosts may have selected for mimetic begging calls in Horsfield's bronze-cuckoos. We quantified species differences in begging call structure from sonograms of nestling vocalizations, by measuring the frequency of the loudest part of the call, its length and its frequency range, and found that the begging calls of shining bronze-cuckoos mimic those of fairy-wren chicks less well than those of Horsfield's bronze-cuckoo chicks (Fig. 3; see also ref. 19). Neither peak frequency (analysis of variance (ANOVA) species × age interaction: $F_{2,21} = 0.40$, $P = 0.66$) nor frequency range (ANOVA species × age interaction: $F_{2,21} = 0.40$, $P = 0.66$) differed significantly between the three species as chicks grew older. However, shining bronze-cuckoo chicks uttered longer calls than fairy-wren offspring, and they became increasingly different from fairy-wren calls as chicks grew older (ANOVA species × age interaction: $F_{2,21} = 8.20$, $P = 0.002$; shining bronze-cuckoo versus superb fairy-wren, Fisher protected least significant difference (PLSD), $P = 0.03$, whereas Horsfield's bronze-cuckoos did not differ significantly from fairy-wrens in this respect (Fisher PLSD, $P = 0.40$).

We have yet to determine whether a host's ability to discriminate against cuckoo chicks is innate or acquired. Great reed warbler *Acrocephalus arundinaceus* cuckoo hosts imprint on the appearance of their first clutch during egg laying and thereafter reject any eggs that appear odd by comparison[4]. However, similarly learnt nestling recognition cannot evolve among hosts of evictor cuckoos because the cost of misimprinting on a lone cuckoo chick, and ever after rejecting host young, outweighs the benefits of avoiding exploitation[6]. According to Lotem's hypothesis[6], females that accept cuckoos must have misimprinted on them during their first breeding attempt and should subsequently reject all other young. We found no evidence to support this view. Females that accepted a Horsfield's bronze-cuckoo nestling did not abandon a lone fairy-wren chick in a later breeding attempt (0 desertions in six cases, binomial test, $P = 0.03$).

Why are superb fairy-wrens apparently unique among hosts of ejector cuckoos in their ability to desert cuckoo nestlings? The cost of accepting a parasitic chick is proportional to the likelihood of finding a cuckoo chick in the nest. Therefore it depends on the incidence of parasitism and the strength of host defences at the egg stage, and so may be greater for fairy-wrens than for other hosts. For example, British reed warbler *Acrocephalus scirpaceus* hosts of the European cuckoo *Cuculus canorus* reject roughly 20% of cuckoo eggs added to their nests, which means that 5–13% of hosts end up rearing a cuckoo chick[3]. By contrast, 13–37% of superb fairy-wren nests monitored at three populations across New South Wales contained Horsfield's bronze-cuckoo eggs (this study; see also refs 20, 21). Even allowing for mistimed egg laying by female Horsfield's bronze-cuckoos, and consequent nest abandonment by hosts, fairy-wrens seem more likely to encounter a cuckoo chick than British reed warblers.

Furthermore, fairy-wren hosts may stand to gain greater net benefits than other hosts by abandoning cuckoo young. The breeding season of superb fairy-wrens is longer (three–six months[22]) than that of a typical European cuckoo host (for example, reed warbler, 2.5 months[23]), so fairy-wrens are better able to capitalize on chick
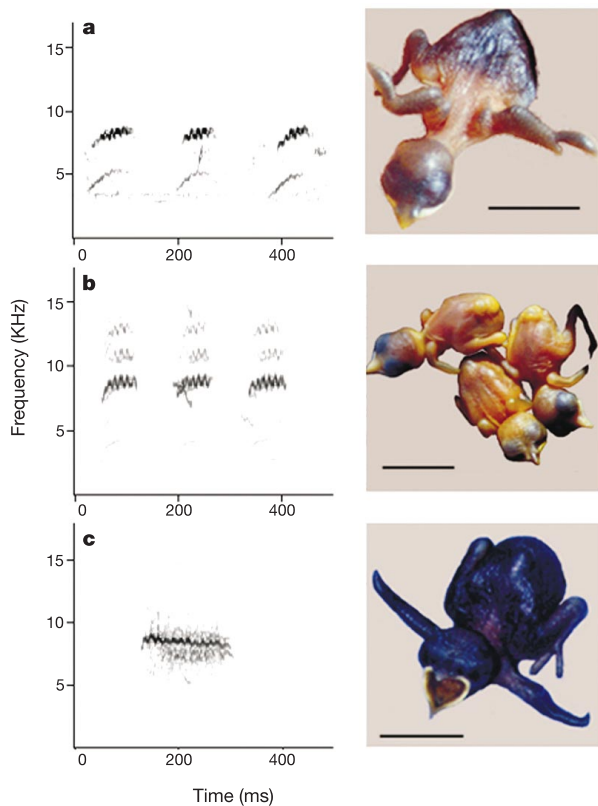
Figure 3 Sonograms from begging calls recorded six days after hatching from a Horsfield's bronze-cuckoo chick (**a**), a brood of three superb fairy-wren chicks (**b**) and a shining bronze-cuckoo chick (**c**). Begging calls of nestling Horsfield's bronze-cuckoos ($N = 7$ recordings from 4 chicks), shining bronze-cuckoos ($N = 5$ recordings from 2 chicks) and superb fairy-wren broods ($N = 14$ recordings from 8 broods) were analysed with Canary 1.2.1. Photographs show the same species 1–2 days after hatching. The photograph in **b** shows two superb fairy-wren chicks (left and right) with a pale morph shining bronze-cuckoo chick (centre). Scale bars, 10 mm.

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desertion by re-nesting. In addition, fairy-wrens might more easily bear the costs, revealed by our experiments, of mistakenly rejecting lone host young. For example, the incidence of host broods with a single chick among superb fairy-wren (3.08% of 1,587 broods; A. Cockburn, personal communication) and reed warbler (3.8% of 2,094 broods[3,24]) broods is similar, and both species rear one to two fledglings per nest[22,23]. However, fairy-wrens can rear up to three broods per year (34.4% of females rear two broods successfully[25]), yielding 2.6–3.9 fledglings on average[14,20,21,25]. By contrast, only 8–32% of reed warblers have a second brood[23]. Thus a single chick represents a relatively smaller fraction of reproductive success for a fairy-wren than a reed warbler.

In short, we predict that cuckoo chick discrimination will evolve only when cuckoos have completely evaded host defences at the egg stage, and only then when parasitism rates are sufficiently high to outweigh the costs of recognition errors, breeding seasons are sufficiently long to allow re-nesting, and hosts have sufficiently high fecundity to bear the cost of mistakenly deserting single chicks of their own. □

Methods

Study species

Cooperatively breeding superb fairy-wren groups comprise up to four males and one breeding female, who alone builds the nest and incubates the clutch[22]. They are a primary host of the Horsfield's bronze-cuckoo[26]. The shining bronze-cuckoo and the fan-tailed cuckoo (*Cacomantis flabelliformis*), occasional fairy-wren brood parasites[26], were both present at our study site but neither parasitized our ringed population during the study.

Egg colour measurement

We measured spectral reflectance of unincubated host and cuckoo eggs using a narrow-ended (2.5-mm diameter) UV-VIS unidirectional reflectance probe, attached to a USB2000 spectroradiometer and PX-2 Xenon strobe (all from Ocean Optics Inc). During measuring, eggs were replaced with model eggs, which were removed when real eggs were returned. We took six measurements at randomly chosen locations within each of three regions (base, middle and tip; 18 readings per egg). The probe illuminated areas approximately 1.5 mm in diameter. Reflectance was calculated relative to a Spectralon 99% reflectance standard between 300 and 700 nm. To prevent egg damage, we added a rubber tip, which extended 2 mm beyond the end of the steel-cased probe. The probe was held perpendicular to the surface of the egg and measurements were taken under a light-proof sheet. Owing to the fineness of the speckle, all reflectance spectra include both white background (spectrally flat) and brown speckle (increasing reflectance across the spectrum, with triple peaks at long wavelengths).

Egg experiments

Both model and real eggs were used in 100 egg discrimination tests ($N = 63$ female fairy-wrens). Model eggs were made of Alumilite super plastic ($N = 22$ small (fairy-wren size: 16 × 12 mm) blue; 11 small parchment; 15 large (fan-tailed cuckoo size: 20 × 15 mm) parchment), cast in silicone moulds and painted with Daler–Rowney or Plaid acrylic paints (titanium white, cobalt, turquoise, buckskin brown, nutmeg, coffee bean, parchment, moss green). Real eggs ($N = 18$ blue; 12 brown; 18 parchment base, fairy-wren-like brown speckling; 7 parchment base, large brown spotting) were used within 14 days of laying and obtained from captive zebra finches (*Taeniopygia guttata*, $N = 7$, egg size 15 × 11 mm) or superb fairy-wren clutches ($N = 43$ eggs) that had been abandoned or where the clutch size had been reduced for the single chick experiment (see below). A single egg was added to the nest during egg laying ($N = 82$) or early incubation ($N = 18$, 0–9 days into incubation, median of 3 days). No female experienced the same treatment twice or was subjected to more than two treatments. Each nest was used only once. We checked the nest the following day and again five days later to determine the outcome. Depredated nests were excluded. There was no significant difference in the response of hosts to plastic compared to real eggs (3 out of 16 blue real eggs compared to 3 out of 22 blue plastic fairy-wren-sized eggs rejected or deserted; $G^2 = 0.2$, $P = 0.67$), nor was the outcome affected by the timing of parasitism (two rejected out of ten blue real eggs placed during laying compared to one out of seven during incubation; $\chi^2 = 0.03$, 1 d.f., $P < 0.99$). We caged 124 out of 734 nests found with garden mesh during incubation. This significantly reduced nest depredation (28% caged, 66% uncaged; $\chi^2 = 46.2$, 1 d.f., $P < 0.0001$) and did not cause chick desertion: we performed daily nest watches on 15 superb fairy-wren broods in caged nests and none was deserted. The light availability inside active fairy-wren nests was measured between 11:00 and 13:00 Eastern Standard Time in full sunlight using a Kyoritsu illuminometer 5200.

Chick experiments

Chick desertion was not caused by interference at the nest. Twenty-six nests containing cuckoo chicks were checked once on hatching day and thereafter their fate was monitored with 1-h nest watches conducted almost daily roughly 50 m from the nest. The nest was not approached again until the chick was deserted ($N = 10$), preyed on ($N = 9$) or fledged ($N = 7$). Eighteen control fairy-wren nests containing unmanipulated broods were subjected to the same treatment and none was deserted.

To create broods of single fairy-wrens, we reduced clutches to a single egg plus two plastic model fairy-wren eggs during incubation. Model eggs were removed within 48 h of hatching. Shining bronze-cuckoo eggs were found in nests of yellow-rumped (*Acanthiza chrysorrhoa*) or buff-rumped thornbills (*A. reguloides*) and transferred to fairy-wren nests before or during incubation. Horsfield's bronze-cuckoo eggs were similarly transferred between fairy-wren nests. After hatching, daily nest watches were essential to detect desertion, because corpses were quickly dispatched by meat ants and thereafter desertion could not be reliably distinguished from depredation. Our experiments were conducted with ethics approval from the Australian National University Animal Experimentation Ethics Committee.

Nestling calls were recorded for 45 min per day, 3–6 days after hatching, with a Sony tie-clip microphone (ECM-T7), clipped within 30 cm of the nest, and connected by a 5-m extension cable to a Sony Professional Walkman (WM-D6C).

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