

Original Article

“Jack-of-all-trades” egg mimicry in the brood parasitic Horsfield’s bronze-cuckoo?

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Parasitism of multiple host species by a generalist poses the difficulty of overcoming a potentially diverse array of host defenses. In some generalist avian obligate brood parasites, selection for egg mimicry by hosts has given rise to host-specific races (gentes), each of which lays an egg that mimics that of its favored host. However, it is unknown how generalist parasites lacking races are able to circumvent egg rejection by hosts. The Horsfield’s bronze-cuckoo, *Chalcites basalis*, is a generalist brood parasite that exploits a diversity of hosts yet is reported to lay monomorphic eggs. Using reflectance spectrometry and visual modeling, we tested for egg polymorphisms in Horsfield’s bronze-cuckoo eggs laid in the nests of 17 host species. We found that the host species possess broadly similar egg phenotypes that differ subtly but significantly from one another in their color and luminance. However, the Horsfield’s bronze-cuckoo does not mimic this diversity, thus ruling out the existence of host-specific egg color and luminance phenotypes that are visible to birds but hidden from humans. Instead, our analyses support the idea that the Horsfield’s bronze-cuckoo egg is a jack-of-all-trades mimic, lying in an intermediate position in avian visual space between the eggs of its various hosts. We suggest that jack-of-all-trades mimicry may be favored among brood parasites that parasitize hosts with a narrow range of egg phenotypes and where individual female brood parasites exploit multiple host species.

Key words: adaptation, arms race, bird color space, brood parasitism, coevolution, cuckoo, egg mimicry, spectrophotometry, tetrachromatic, TETRACOLORSPACE.

INTRODUCTION

The cost of attack by a parasite is well known to select hosts that can effectively defend themselves (Thompson 2005). Host defenses, in turn, require specific counteradaptations in the parasite if it is to persist in exploiting the host, and the pattern of reciprocating adaptation and counteradaptation can lead to a coevolutionary arms race between host and parasite (Dawkins and Krebs 1979). Selection tailors specialist parasites to specifically exploit their particular host (Kaltz and Shykoff 1998); however, generalist parasites, which exploit a diversity of host species, face a challenge as they must overcome the potentially unique defenses of multiple host species.

In some cases, generalist species comprise a collection of genetically differentiated populations, each of which has become specialized on a single host species (Thompson 1994). Avian obligate brood parasites, which impose the cost of raising offspring on their hosts, provide a good example. The common cuckoo, *Cuculus*

canorus, parasitizes multiple species and the different host species lay eggs with different phenotypes. Hosts defend themselves against parasitism by rejecting eggs that look unlike their own and this has favored the evolution of genetically distinct host-specific races in the cuckoo, each laying an egg that matches its respective host species (Brooke and Davies 1988; Moksnes and Røskaft 1995; Gibbs et al. 2000; Stoddard and Stevens 2010, 2011). Divergence into host-specific races is also common among other avian obligate brood parasites (reviewed by Langmore and Spottiswoode 2012). However, some avian obligate brood parasites, such as cowbirds, do not appear to have mimetic eggs (Rothstein 1975; Peer and Sealy 2004). It is suspected that this may be due to the lack of defenses by recently colonized hosts (“evolutionary-lag” hypothesis: Rothstein 1982; Stokke et al. 2002; Peer and Sealy 2004), hosts that are physically unable to defend against parasitism (Rohwer and Spaw 1988; but see Underwood and Sealy 2006), or that acceptance of parasitic eggs can be beneficial to the host in some instances (Sato et al. 2010; Gloag et al. 2012; Canestrari et al. 2014). By and large, how generalist parasites that have not diverged into host-specific races have adapted to their hosts is less well understood.

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The Horsfield's bronze-cuckoo, *Chalcites basalis*, is a generalist brood parasite in Australia. It primarily parasitizes fairy-wrens (*Malurus* spp.) throughout its range but also regularly exploits at least 27 additional host species (Brooker and Brooker 1989). To human eyes, Horsfield's bronze-cuckoo eggs appear monomorphic (however, see Campbell 1906) and approximately similar to the eggs laid by almost all of its major hosts; the shell has a white ground color with reddish-brown speckling (Figure 1). This is perhaps a little surprising given the broad diversity generally apparent in passerine eggs (Kilner 2006). Previous work has demonstrated that Horsfield's bronze-cuckoo egg morphology is not the outcome of competition between female cuckoos (Langmore and Kilner 2009). Therefore, we focus on the most likely explanation for the similarity between cuckoo and host egg types: selection by hosts.

Australian bronze-cuckoo hosts are generally less likely to reject odd-looking eggs than their European counterparts (Langmore et al. 2005), though their level of egg rejection is theoretically sufficient to select for mimetic cuckoo eggs (Davies 2000). Unlike the common cuckoo (Gibbs et al. 2000), there is no genetic evidence to suggest that the Horsfield's bronze-cuckoo has segregated into distinct host races (Joseph et al. 2002; Langmore et al. 2008). However, these analyses do not rule out the possibility that the Horsfield's bronze-cuckoo has, in fact, segregated into host races, but too recently to be detectable (Joseph et al. 2002). If so, these host races may be recognizable through subtle differences in egg color that mimic those of their respective hosts but are difficult to discern with human eyes. Equivalent "hidden" races have been found through use of more objective color measurements in the Australian pallid cuckoo, *Cuculus pallidus* (Starling et al. 2006).

A previous description of the Horsfield's bronze-cuckoo's egg in different host nests indeed suggested that exactly such subtle diversification might exist (Campbell 1906), though this possibility has yet to be tested with modern techniques for objective color measurement. In this study, we investigate whether the Horsfield's bronze-cuckoo has evolved host-specific egg phenotypes. The 2 key predictions of this hypothesis are that 1) hosts differ in their egg coloration, perhaps as a function of their different nest structures and 2) cuckoo eggs also vary in their coloration, to match those laid by their favored host.

MATERIALS AND METHODS

Data collection

We obtained reflectance spectra from 1 Horsfield's bronze-cuckoo and 1 randomly selected host egg from each of 231 parasitized clutches at the Australian Wildlife Collection, Canberra, Australia, and the Australian Museum, Sydney, Australia, between January and March 2012. We only included species for which we could obtain a minimum of 6 parasitized clutches. Clutches comprised 17 hosts of the Horsfield's bronze-cuckoo: red-backed fairy-wren (*Malurus melanocephalus*, $n = 9$), splendid fairy-wren (*Malurus splendens*, $n = 12$), superb fairy-wren (*Malurus cyaneus*, $n = 57$), variegated fairy-wren (*Malurus lamberti*, $n = 10$), white-winged fairy-wren (*Malurus leucopterus*, $n = 16$), brown thornbill (*Acanthiza pusilla*, $n = 13$), buff-rumped thornbill (*Acanthiza reguloides*, $n = 13$), chestnut-rumped thornbill (*Acanthiza uropygialis*, $n = 6$), striated thornbill (*Acanthiza lineata*, $n = 13$), yellow thornbill (*Acanthiza nana*, $n = 7$), yellow-rumped thornbill (*Acanthiza chrysorrhoa*, $n = 14$), grey fantail (*Rhipidura albiscapa*, $n = 7$), pacific robin (*Petroica multicolor*, $n = 6$), red-capped

robin (*Petroica goodenovii*, $n = 13$), speckled warbler (*Pyrrholaemus sagittatus*, $n = 18$), white-browed scrubwren (*Sericornis frontalis*, $n = 11$), and the white-fronted chat (*Epthianura albifrons*, $n = 7$). We used all available clutches for each species, except we excluded all but one of the clutches collected in the same location and year to minimize the chance of pseudoreplication. The majority of the eggs were collected between 1890 and 1950. Although the grey fantail is not considered a common host of this cuckoo species, it was included in the analysis as it is an occasional host, and there was an adequate sample size available for use (Brooker and Brooker 1989). We used nest descriptions from the Handbook of Australian, New Zealand and Antarctic Birds (Higgins 1999; Higgins et al. 2001; Higgins and Peter 2002) to classify species as "dome nesters" or "cup nesters"; all had dome nests except for the pacific and red-capped robins, white-fronted chat, and grey fantail, which have cup nests.

Spectral measurements of eggs

To quantify egg phenotype objectively, we focused on 2 aspects of cuckoo egg appearance, namely color and luminance. Reflectance spectra for each egg were obtained using an Ocean Optics Jaz™ spectrometer relative to an Ocean Optics™ 99% white reflectance standard. Measurements were taken at a constant distance and a 45° angle using a narrow ended UV-Vis unidirectional Ocean Optics™ reflectance probe (QR400-7-SR). As Horsfield's bronze-cuckoo eggs (and those of many of their hosts) are very densely speckled (Figure 1), we were unable to distinguish between "background" and "speckle" colors while taking measurements. Consequently, we took 3 randomly placed measures each from the top, middle, and the bottom of each cuckoo and host egg. The 9 measurements were subsequently averaged to obtain an average egg color for analysis (similar to Stoddard and Stevens 2011).

Modeling receptor stimulation in avian tetrahedral color space

There are 2 main classes of color vision in birds, with birds possessing either ultraviolet-sensitive (UVS) or violet-sensitive (VS) cones (Cuthill 2006). Most passeriformes (excluding Corvidae, Tyrannidae, Meliphagidae, and Thamnophilidae) are considered to have UVS-sensitive visual systems (Ödeen and Håstad 2003, 2010) although recent research indicates that the distribution of UVS sensitivity within Passeriformes is much more complex than previously believed (Ödeen and Håstad 2003). Because some primary hosts of the Horsfield's bronze-cuckoo possess UVS (superb, splendid, and variegated fairy-wrens), whereas others possess VS (red-backed and white-winged fairy-wrens) or not yet described (brown, buff-rumped, chestnut-rumped, striated, yellow, and yellow-rumped thornbills; grey fantail, pacific, and red-capped robins; speckled warbler, white-browed scrubwren, and white-fronted chat) visual systems (Ödeen et al. 2012), we used both UVS and VS models for all of our analyses (see Table 1 for summary data). We used the visual system of the blue tit (*Parus caeruleus*) to model UVS vision (Hart et al. 2000) and the peafowl (*Pavo cristatus*) to model VS vision (Hart 2001).

For each egg, we calculated the cone stimulation (photon catch) values for the ultraviolet-sensitive (UVS) or violet-sensitive (VS), shortwave-sensitive (SWS), mediumwave-sensitive (MWS), and longwave-sensitive (LWS) cones (color) and double (DCS) cones (luminance) (Table 1) using TETRACOLORSPACE for MATLAB software (Stoddard and Prum 2008; Stoddard and Stevens 2011). We subsequently analyzed egg colors (based on the UVS or

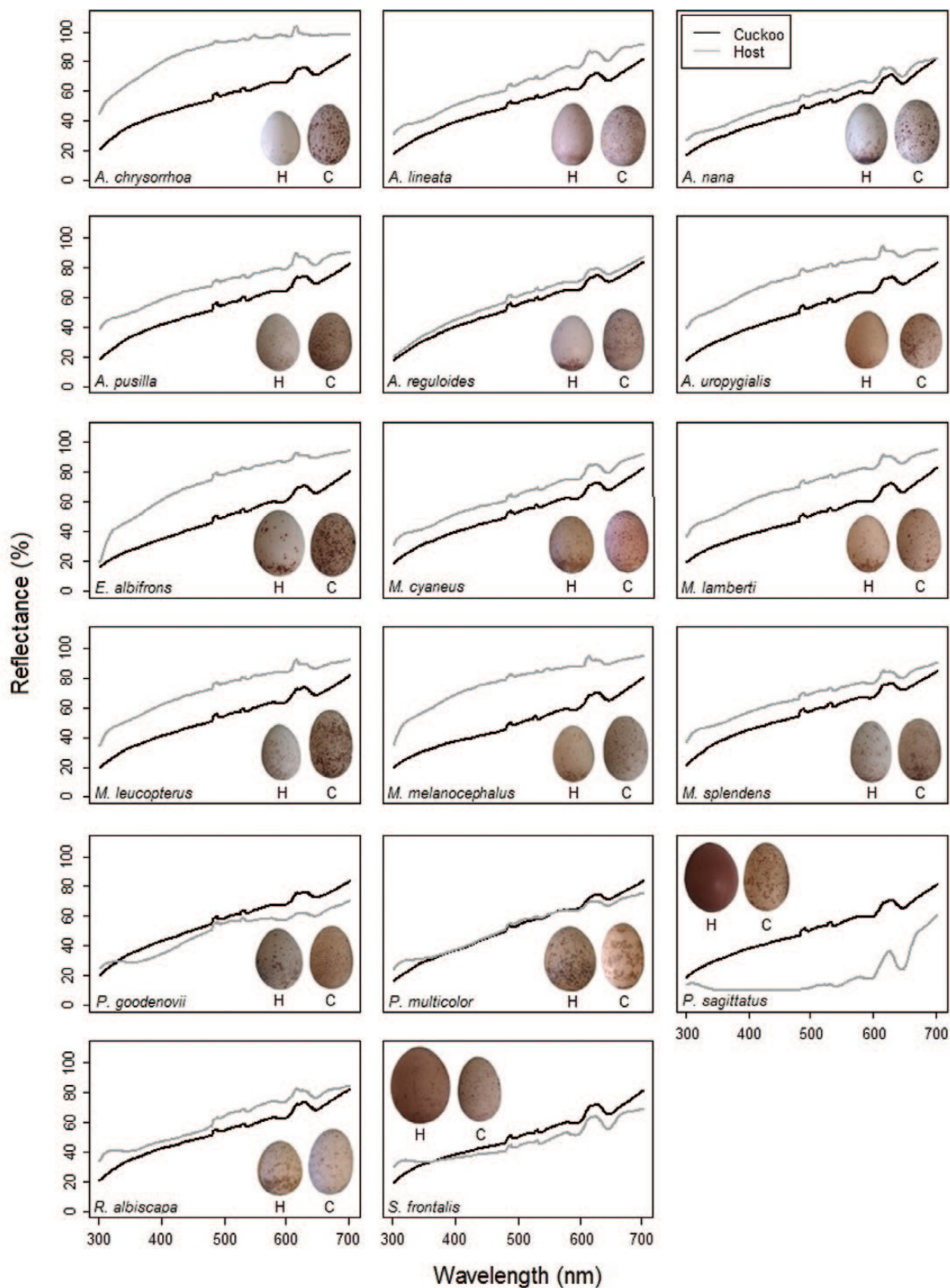


Figure 1

Average spectral reflectance, and a host and corresponding Horsfield's bronze-cuckoo egg (C and H, respectively) for each of the 17 investigated species. Dotted lines denote standard errors.

Table 1
Summary data describing cuckoo and host egg colors

Species	Spectral sensitivity of host	<i>n</i>	UV/V	S	M	L	DC	Color: JND ± SE	Luminance: JND ± SE	Nest type
Superb fairy-wren	UVS	57	0.1736	0.2259	0.2744	0.326	0.7203	3.23 ± 1.25	6.77 ± 0.37	Dome
Superb fairy-wren-cuckoo		57	0.1618	0.2289	0.2805	0.3287	0.5984			
Striated thornbill	UVS	13	0.169	0.2274	0.2772	0.3263	0.7284	2.48 ± 0.76	5.13 ± 0.70	Dome
Striated thornbill-cuckoo		13	0.1588	0.2289	0.2814	0.331	0.5912			
Striated thornbill	VS	13	0.169	0.2274	0.2772	0.3263	0.7322	1.99 ± 0.72	5.16 ± 0.70	
Striated thornbill-cuckoo		13	0.1588	0.2289	0.2814	0.331	0.5937			
White-winged fairy-wren	VS	16	0.2076	0.2405	0.264	0.2879	0.8185	2.74 ± 1.22	7.53 ± 0.75	Dome
White-winged fairy-wren-cuckoo		16	0.1911	0.2335	0.2669	0.3085	0.6119			
Splendid fairy-wren	UVS	12	0.1853	0.2363	0.2726	0.3058	0.7446	3.23 ± 0.88	5.99 ± 0.61	Dome
Splendid fairy-wren-cuckoo		12	0.1674	0.2308	0.2794	0.3224	0.6425			
Brown thornbill	UVS	13	0.186	0.2337	0.2711	0.3091	0.7676	3.23 ± 1.08	6.89 ± 0.88	Dome
Brown thornbill-cuckoo		13	0.1639	0.2305	0.2805	0.3251	0.6153			
Brown thornbill	VS	13	0.2062	0.2356	0.2613	0.297	0.7708	2.62 ± 1.03	6.92 ± 0.89	
Brown thornbill-cuckoo		13	0.1928	0.2338	0.2662	0.3071	0.6182			
Pacific robin	UVS	6	0.1522	0.2251	0.2907	0.332	0.6122	1.94 ± 0.59	4.48 ± 1.12	Cup
Pacific robin-cuckoo		6	0.1465	0.226	0.2888	0.3388	0.6156			
Pacific robin	VS	6	0.1777	0.2351	0.2748	0.3124	0.6182	1.62 ± 0.50	4.48 ± 1.14	
Pacific robin-cuckoo		6	0.1796	0.2317	0.2718	0.317	0.6197			
Variegated fairy-wren	UVS	10	0.1839	0.2348	0.2727	0.3087	0.7967	3.45 ± 0.47	7.23 ± 0.63	Dome
Variegated fairy-wren-cuckoo		10	0.1618	0.2249	0.2798	0.3335	0.5788			
Buff-rumped thornbill	UVS	12	0.1802	0.2398	0.2751	0.3048	0.8097	3.23 ± 1.01	6.41 ± 0.73	Dome
Buff-rumped thornbill-cuckoo		12	0.1567	0.23	0.2843	0.329	0.6187			
Buff-rumped thornbill	VS	12	0.2066	0.24	0.2629	0.2904	0.8136	2.54 ± 0.84	6.41 ± 0.74	
Buff-rumped thornbill-cuckoo		12	0.1885	0.2337	0.2685	0.3093	0.6223			
White-browed scrubwren	UVS	11	0.1872	0.2118	0.2632	0.3378	0.4998	4.03 ± 2.00	10.01 ± 1.14	Dome
White-browed scrubwren-cuckoo		11	0.1658	0.2232	0.2772	0.3338	0.571			
White-browed scrubwren	VS	11	0.1925	0.2197	0.2582	0.3296	0.5008	3.34 ± 2.13	9.21 ± 1.21	
White-browed scrubwren-cuckoo		11	0.1893	0.2283	0.265	0.3174	0.5731			
White-fronted chat	UVS	7	0.174	0.2431	0.2798	0.3031	0.8393	3.87 ± 1.33	8.52 ± 0.61	Cup
White-fronted chat-cuckoo		7	0.1519	0.2258	0.2851	0.3373	0.5714			
White-fronted chat	VS	7	0.2054	0.2424	0.2654	0.2868	0.8447	3.14 ± 0.59	8.53 ± 0.64	
White-fronted chat-cuckoo		7	0.1827	0.2309	0.2694	0.3169	0.5748			
Chestnut-rumped thornbill	UVS	6	0.1851	0.2415	0.2751	0.2983	0.8314	3.59 ± 1.07	6.94 ± 1.15	Dome
Chestnut-rumped thornbill-cuckoo		6	0.1574	0.2287	0.2835	0.3303	0.6045			
Chestnut-rumped thornbill	VS	6	0.2099	0.2419	0.2634	0.2848	0.836	2.85 ± 0.90	6.95 ± 1.17	
Chestnut-rumped thornbill-cuckoo		6	0.1879	0.2327	0.2683	0.3111	0.608			
Red-capped robin	UVS	13	0.1562	0.2415	0.2918	0.3105	0.6498	2.52 ± 0.88	5.16 ± 0.81	Cup
Red-capped robin-cuckoo		13	0.1617	0.232	0.2834	0.323	0.5711			
Red-capped robin	VS	13	0.1861	0.2492	0.2737	0.2909	0.6539	2.35 ± 0.75	5.16 ± 0.81	
Red-capped robin-cuckoo		13	0.1911	0.236	0.2684	0.3045	0.576			
Red-backed fairy-wren	VS	9	0.2163	0.2438	0.2608	0.2792	0.8583	3.61 ± 1.58	9.51 ± 1.58	Dome
Red-backed fairy-wren-cuckoo		9	0.1875	0.2278	0.2663	0.3183	0.5802			
Yellow thornbill	UVS	7	0.1702	0.2223	0.2713	0.3361	0.6376	3.29 ± 0.78	9.28 ± 0.82	Dome
Yellow thornbill-cuckoo		7	0.1569	0.2252	0.2813	0.3366	0.5672			
Yellow thornbill	VS	7	0.1915	0.226	0.2606	0.3219	0.6404	3.03 ± 0.86	8.96 ± 0.75	
Yellow thornbill-cuckoo		7	0.1854	0.2299	0.2669	0.3177	0.5696			
Yellow-rumped thornbill	UVS	14	0.1981	0.2531	0.2705	0.2783	0.9568	3.82 ± 1.16	8.68 ± 0.78	Dome
Yellow-rumped thornbill-cuckoo		14	0.1696	0.2323	0.2773	0.3207	0.6364			
Yellow-rumped thornbill	VS	14	0.2246	0.2495	0.2594	0.2665	0.9607	3.26 ± 1.04	8.61 ± 0.86	
Yellow-rumped thornbill-cuckoo		14	0.1966	0.2352	0.2641	0.3041	0.6387			
Grey fantail	UVS	7	0.172	0.2226	0.2839	0.3215	0.6864	3.32 ± 0.85	6.42 ± 1.24	Cup
Grey fantail-cuckoo		7	0.1664	0.2278	0.2781	0.3277	0.6053			
Grey fantail	VS	7	0.1879	0.233	0.2721	0.3069	0.7106	2.98 ± 0.83	6.46 ± 1.26	
Grey fantail-cuckoo		7	0.1922	0.2319	0.2651	0.3108	0.6075			
Speckled warbler	UVS	18	0.1676	0.1607	0.2298	0.4419	0.1787	9.19 ± 2.71	24.89 ± 1.95	Dome
Speckled warbler-cuckoo		18	0.1626	0.2271	0.2789	0.3314	0.5742			
Speckled warbler	VS	18	0.1577	0.171	0.2315	0.4399	0.1735	9.22 ± 2.93	25.66 ± 2.02	
Speckled warbler-cuckoo		18	0.19	0.2311	0.2653	0.3137	0.5764			

Both UVS and VS summary data are presented for the species whose visual systems are not known. Shown here are sample size (*n*), relative stimulation values for the ultraviolet-sensitive (UVS) or violet-sensitive (VS), shortwave-sensitive (SWS), mediumwave-sensitive (MWS), longwave-sensitive (LWS), and double cone (DCS) sensitive cone types, as well as color and luminance JNDs and nest type.

VS, SWS, MWS, and LWS relative cone stimulation values) in avian tetrahedral color space using TETRACOLORSPACE for MATLAB and R v2.13.2 (R Development Core Team 2011). We

complemented this analysis by calculating color and luminance “just-noticeable differences (JNDs)” using custom code (following Vorobyev and Osorio 1998).

First, to investigate whether Horsfield's bronze-cuckoo eggs varied in color when sorted by host or host nest architecture, and whether host eggs varied in color when sorted by species or nest architecture, we compared the relative cone stimulation values (egg color: UVS or VS, SWS, MWS, and LWS). To investigate whether Horsfield's bronze-cuckoo eggs varied in luminance when sorted by host or host nest architecture, and whether host eggs varied in luminance when sorted by species or nest architecture, we compared the absolute double cone stimulation values (egg luminance: DCS).

Next, we investigated whether the color of cuckoo eggs was better matched to a subset of host species. We calculated the X , Y , Z coordinate for each cuckoo and respective host egg in avian tetrahedral color space (Endler and Mielke 2005; Stoddard and Prum 2008; Stoddard and Stevens 2011). We then calculated the centroids of the cuckoo and various host egg color distributions and used the distances in avian tetrahedral color space between the cuckoo and respective host centroids of the various hosts as a simple measure of the color difference between the cuckoo and corresponding host eggs. To complement this analysis, we determined whether cuckoo and host egg color and luminance differences were distinguishable by calculating color and luminance differences in terms of JNDs (Vorobyev and Osorio 1998). A JND of less than 3 is considered difficult to distinguish under good light conditions (Vorobyev and Osorio 1998; Siddiqi et al. 2004). Although the species investigated in this study use both dome and open nests (Table 1), we did not account for the light environment of the nest(s) in our analyses; this would make direct comparisons between all species difficult. Consequently, as the majority of host species of the Horsfield's bronze-cuckoo build dome nests (with exceptions of the pacific and red-capped robins, grey fantail, and white-fronted chat that build cup nests), measures of perceived differences between cuckoo and host eggs are likely overestimates as phenotypic differences are easier to identify in good, versus poor, light conditions (Stoddard and Stevens 2011).

STATISTICAL ANALYSIS

To test for variation in 1) host egg color, perhaps as a function of nest structure, and 2) cuckoo egg color in relation to host and host nest architecture, we compared the relative cone stimulation values of eggs using a multiresponse permutation procedure (MRPP; with 999 permutations) in the R package "vegan" with "Manhattan" distance (sum of absolute distances; Oksanen et al. 2011). MRPP is a nonparametric multivariate statistical technique that is robust to nonnormally distributed data, unequal variance, and unbalanced designed through use of permutations between groups and is used to calculate whether there is a difference between groups of entities, in our case, relative cone stimulation values (egg color) and host species or nest architecture (Zimmerman et al. 1985; Endler and Mielke 2005; Carter and Feeney 2012). Following the recommendations of Endler and Mielke (2005), who used comparable methods to make comparisons of avian color patterns, we performed analyses on relative cone stimulation values (see Table 1 for summary data). To test for variation in 1) host egg luminance, perhaps as a function of nest structure, and 2) cuckoo egg luminance in relation to host and host nest architecture, we compared the absolute double cone stimulation values of the cuckoo and respective host eggs using nonparametric Kruskal–Wallis tests with multiple comparisons post hoc tests. Finally, to test for variation in color between cuckoo and host eggs, we compared the distances between cuckoo and respective host egg color centroids in color space using Kruskal–Wallis tests with multiple comparisons post hoc tests.

RESULTS

Prediction 1: hosts differ in their egg coloration, perhaps as a function of their different nest structures

Host egg color and luminance sorted by species varied significantly in avian color space when considering a UVS visual model

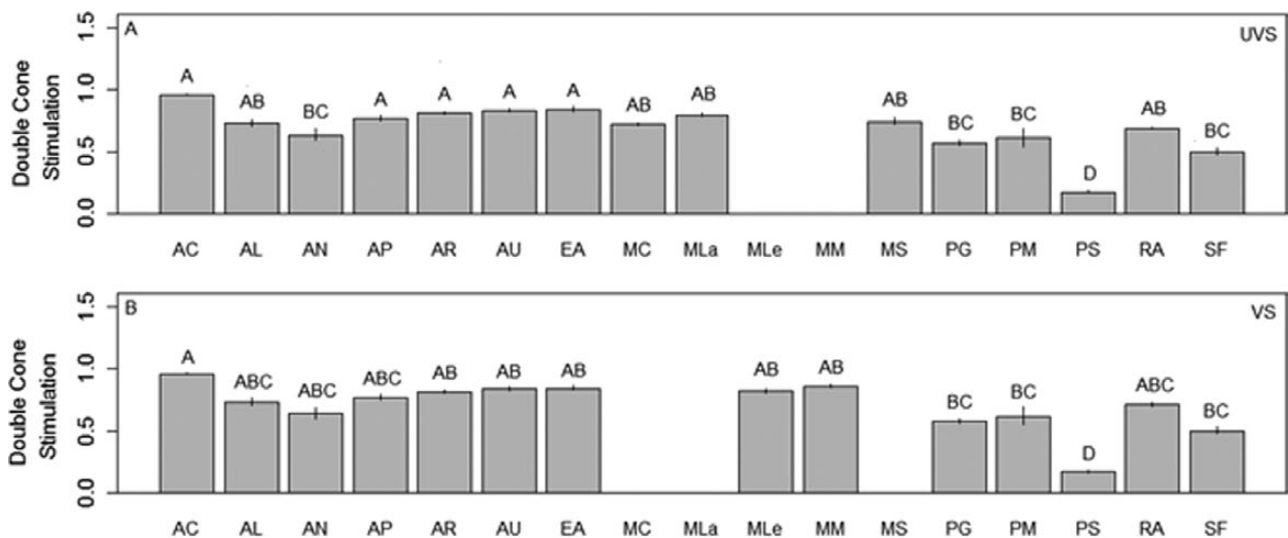


Figure 2 Mean double cone (luminance) stimulation values for host eggs when considering a UVS (A) or VS (B) visual model. Names refer to yellow-rumped thornbill (AC), striated thornbill (AL), yellow thornbill (AN), brown thornbill (AP), buff-rumped thornbill (AR), chestnut-rumped thornbill (AU), white-fronted chat (EA), superb fairy-wren (MC), variegated fairy-wren (MLa), white-winged fairy-wren (MLe), red-backed fairy-wren (MM), splendid fairy-wren (MS), red-capped robin (PG), pacific robin (PM), speckled warbler (PS), grey fantail (RA), and white-browed scrubwren (SF). Error bars denote standard error and different letters denote significant differences ($\alpha = 0.05$).

(MRPP [color]: $A = 0.38$, observed $\delta = 0.068$, expected $\delta = 0.11$, $P < 0.01$) (Kruskal–Wallis test [luminance]: $\chi^2 = 139.70$, $P < 0.01$; see Figure 2A for results of post hoc analysis) or VS visual model (MRPP: $A = 0.502$, observed $\delta = 0.056$, expected $\delta = 0.118$, $P < 0.01$) (Kruskal–Wallis test [luminance]: $\chi^2 = 119.50$, $P < 0.01$; see Figure 2B for results of post hoc analysis). Considering a UVS visual model, MRPP analysis identified 7 groups (i.e., 7 distinctive color clusters) comprising (in order of increasing similarity) 1) speckled warbler; 2) pacific robin; 3) white-browed scrubwren; 4) red-capped robin; 5) yellow-rumped thornbill; 6) splendid fairy-wren, brown thornbill, chestnut-rumped thornbill, buff-rumped thornbill, variegated fairy-wren, and white-fronted chat; and 7) striated thornbill, superb fairy-wren, yellow thornbill, and grey fantail. Considering a VS visual model, MRPP analysis identified 6 groups comprising 1) speckled warbler; 2) white-browed scrubwren; 3) pacific robin; 4) yellow-rumped thornbill, brown thornbill, chestnut-rumped thornbill, buff-rumped thornbill, and white-fronted chat; 5) red-backed fairy-wren and red-capped robin; and 6) striated thornbill, white-winged fairy-wren, yellow thornbill, and grey fantail.

Host egg color and luminance could be explained by variation in nest architecture when considering a UVS visual model (MRPP [color]: $A = 0.03$, observed $\delta = 0.107$, expected $\delta = 0.110$, $P < 0.01$) (Kruskal–Wallis test [luminance]: $\chi^2 = 4.43$, $P = 0.04$) and VS visual model for egg color (MRPP: $A = 0.029$, observed $\delta = 0.114$, expected $\delta = 0.118$, $P < 0.01$). However, there was no difference in host egg luminance when considering a VS visual model (Kruskal–Wallis test [luminance]: $\chi^2 = 3.32$, $P = 0.07$).

Prediction 2: cuckoo eggs also vary in their coloration to match those laid by their favored host

By contrast, the color and luminance of Horsfield's bronze-cuckoo eggs, sorted by parasitized host, did not vary significantly when considering either UVS (MRPP [color]: $A < 0.01$, observed $\delta = 0.062$, expected $\delta = 0.063$, $P = 0.33$) (Kruskal–Wallis test [luminance]: $\chi^2 = 13.07$, $P = 0.52$) or VS (MRPP [color]: $A < 0.01$, observed $\delta = 0.117$, expected $\delta = 0.118$, $P = 0.32$) (Kruskal–Wallis test [luminance]: $\chi^2 = 9.14$, $P = 0.76$) visual model.

Horsfield's bronze-cuckoo egg color and luminance, sorted by host nest architecture, also did not vary when considering a UVS (MRPP [color]: $A < 0.01$, observed $\delta = 0.063$, expected $\delta = 0.063$, $P = 0.57$) (Kruskal–Wallis test [luminance]: $\chi^2 = 1.04$, $P = 0.31$) or VS (MRPP: $A < 0.01$, observed $\delta = 0.118$, expected $\delta = 0.118$, $P = 0.52$) (Kruskal–Wallis test [luminance]: $\chi^2 = 1.18$, $P = 0.28$) visual model, indicating that there are no host-specific egg races based on egg color or luminance in this cuckoo (Figure 1).

The monomorphic Horsfield's bronze-cuckoo eggs were located in an intermediate position in avian color space between the eggs of its various hosts (Figure 3A,D and Supplementary Figures 1 and 2). When considering a UVS visual model, the distances between the cuckoo and host centroids in avian color space were not significantly different from one another with exception of 2 host species (speckled warbler and yellow-rumped thornbill) (Kruskal–Wallis test: $\chi^2 = 85.38$, $P < 0.0001$; see Figure 3A for results of post hoc analysis). When considering a VS visual model, the distances between the cuckoo and host centroids in avian color space were not different from one another with exception of 1 host species (speckled warbler) (Kruskal–Wallis test: $\chi^2 = 67.69$, $P < 0.0001$; see Figure 3D for results of post hoc analysis).

JNDs between cuckoo and host eggs

The JNDs in color and luminance between the monomorphic Horsfield's bronze-cuckoo and respective host eggs were similar among the majority of cuckoo–host pairs. With the exception of the speckled warbler, under this model, the color of all cuckoo eggs would be difficult to distinguish from their corresponding host eggs in good light conditions when considering either a UVS or VS visual model (less than or within error of 3 JNDs; Table 1 and Figure 3B,E). By contrast, according to our analyses, the luminance of all cuckoo eggs would be distinguishable from their corresponding host eggs in good light conditions when considering either a UVS or VS visual model (greater than 3 JNDs; Table 1 and Figure 3C,F).

DISCUSSION

Our analyses revealed that host eggs did vary subtly from one another in their coloration, partly as a function of nest architecture. However, we could find no evidence that the Horsfield's bronze-cuckoo tracks this variation by laying host-specific or nest type-specific egg morphs (Figures 1, 2A,B, and 3A–F). By contrast, except when compared to the speckled warbler and to a lesser extent the yellow-rumped thornbill, the Horsfield's bronze-cuckoo eggs measured in this study occupy a position in avian color space intermediate between the rather similar eggs of its various hosts and were perceived to differ from host eggs in color and luminance from the perspectives of hosts with UVS or VS visual systems (Figure 3A–F). Although it is important to consider that the cuckoo eggs available for use in this study may be biased toward being more similar to those of their hosts, as those that are less similar may have been rejected by the hosts prior to collection, this is a problem inherent to all museum egg collections. Further, this is unlikely to be an important problem for this particular study as we found that Horsfield's bronze-cuckoo eggs were monomorphic irrespective of parasitized host species, and the hosts of this cuckoo rarely reject eggs (with exception of the grey fantail; Langmore et al. 2005).

These findings suggest an alternative explanation for the mimetic eggs of the Horsfield's bronze-cuckoo; the moderate similarity between Horsfield's bronze-cuckoo and host eggs represents a “compromise” egg type to overcome the defenses of multiple host species (Edwardsen et al. 2001; Stoddard and Stevens 2010). Theoretical analyses show that when there is selection for mimicry of multiple models, and the models are sufficiently similar to one another, then mimetic polymorphism is very unlikely (Sherratt 2002). Instead, a “jack-of-all-trades” mimic is favored, one that lies closest to the models most frequently encountered during evolutionary time, but at some intermediate point (Sherratt 2002). Thus, the Horsfield's bronze-cuckoo egg may be a “jack-of-all-trades” intermediate mimic of its hosts.

Together with the findings of previous work, our results suggest that the Horsfield's bronze-cuckoo has an “offence portfolio” of diverse adaptations, which together enable it to pursue a generalist lifestyle without segregating into host-specific races (Joseph et al. 2002; Langmore et al. 2008, 2011). Like many brood parasites (Kilner and Langmore 2011; Feeney et al. 2012), the Horsfield's bronze-cuckoo must be discreet around host nests as detection can result in host aggression and increase the likelihood of egg and chick rejection (Langmore et al. 2009, 2012; Feeney and Langmore 2013; Feeney et al. 2013). However, once the egg is successfully deposited in the host nest, the similar egg

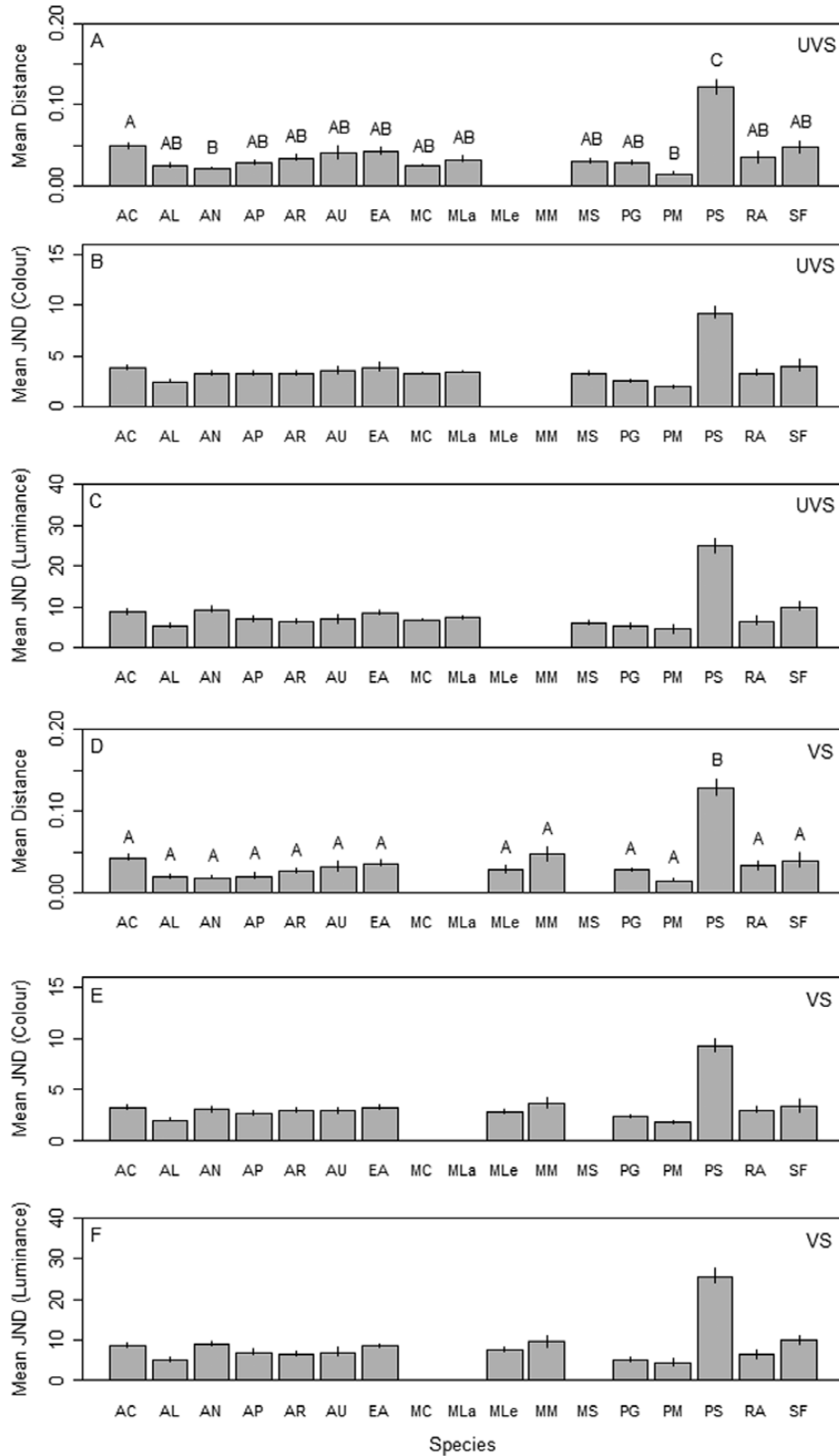


Figure 3

(A) Mean distance between corresponding cuckoo and host color centroids in avian color space (UVS), (B) mean color JND (UVS), (C) mean luminance JND (UVS), (D) mean distance between corresponding cuckoo and host color centroids in avian color space (VS), (E) mean color JND (VS), and (F) mean luminance JND (VS). Names refer to yellow-rumped thornbill (AC), striated thornbill (AL), yellow thornbill (AN), brown thornbill (AP), buff-rumped thornbill (AR), chestnut-rumped thornbill (AU), white-fronted chat (EA), superb fairy-wren (MC), variegated fairy-wren (MLa), white-winged fairy-wren (MLe), red-backed fairy-wren (MM), splendid fairy-wren (MS), red-capped robin (PG), pacific robin (PM), speckled warbler (PS), grey fantail (RA), and white-browed scrubwren (SF). Error bars denote standard error and different letters denote significant differences ($\alpha = 0.05$).

color of the Horsfield's bronze-cuckoo to those of the majority of its host species may help decrease the likelihood of eliciting host defenses (Davies 2000; Langmore et al. 2005). At the nestling stage, Horsfield's bronze-cuckoo nestlings similarly exhibit "jack-of-all-trades" color mimicry of the nestlings of many of its hosts (Langmore et al. 2011), which is adaptive as it reduces the probability of rejection by at least the superb fairy-wren (Langmore et al. 2003). In addition to morphological "jack-of-all-trades" mimicry, Horsfield's bronze-cuckoo chicks show considerable plasticity in their call structure, allowing chicks to modify their begging call to resemble the calls uttered by different hosts (Langmore et al. 2008).

The "jack-of-all-trades" strategy we suggest for the Horsfield's bronze-cuckoo may be a more common strategy in brood parasites than is realized; similar intermediate resemblance between the eggs of cuckoos and some of its secondary host species has been suggested by other studies (Edvardsen et al. 2001; Stoddard and Stevens 2010). Why, then, have some brood parasites evolved a "jack-of-all-trades" strategy, whereas other generalist cuckoos have evolved host-specific races, each of which lays an egg that resembles its favored host? We propose 2 ecological attributes that are likely to predispose brood parasites toward a jack-of-all-trades strategy. First, a narrow range of egg phenotypes in hosts facilitates "jack-of-all-trades" mimicry by preventing the evolution of polymorphic mimics (Sherratt 2002). Diversity in egg morphology among hosts of the Horsfield's bronze-cuckoo was very low, perhaps reflecting the high proportion of hosts that lay their eggs in dark, dome-shaped nests (13 of the 17 measured species). Second, the parasitic ecology of the cuckoo may favor "jack-of-all-trades" generalism rather than mimetic polymorphisms. Theoretical work predicts that "jack-of-all-trades" generalism should evolve when several host species occur in different areas or emerge at different times (Sherratt 2002). Data for the Horsfield's bronze-cuckoo support this prediction; Horsfield's bronze-cuckoos breed over almost the entire Australian continent, are nomadic, opportunistic, and breed wherever conditions are most favorable (Higgins 1999; Langmore and Kilner 2007). Thus, the densities of host species and timing of host breeding would be relatively unpredictable when compared with other, more site-attached cuckoo species (Møller et al. 2011). Unpredictability would also favor flexibility in choice of host species by individual female cuckoos (as has been observed in Horsfield's bronze-cuckoos; Langmore et al. 2007). This flexibility is more easily achieved if the cuckoo possesses a compromise egg type rather than a host-specific egg type.

In summary, we have shown that the Horsfield's bronze-cuckoo has not evolved polymorphic, host-specific egg types. Instead, we suggest that the egg morphology of Horsfield's bronze-cuckoo is consistent with the evolution of a "compromise" egg that is an imperfect mimic of the eggs of its multiple hosts. This would constitute one part of a broader offence portfolio of "jack-of-all-trades" adaptations possessed by the Horsfield's bronze-cuckoo for overcoming the defenses of multiple host species without diverging into host-specific races. This strategy can be explained, at least in part, by the ecology and evolutionary history of the Horsfield's bronze-cuckoo and its hosts.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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REFERENCES

- Brooke M de L, Davies NB. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*. 335:630–632.
- Brooker MG, Brooker LC. 1989. Cuckoo hosts in Australia. *Aust Zool Rev*. 2:1–67.
- Campbell AG. 1906. Observations on the rearing of a cuckoo. *Emu*. 6:120–126.
- Canestrari D, Bolopo D, Turlings TCJ, Röder G, Marcos JM, Baglione V. 2014. From parasitism to mutualism: unexpected interactions between a cuckoo and its host. *Science*. 343:1350–1352.
- Carter AJ, Feeney WE. 2012. Taking a comparative approach: analysing personality as a multivariate behavioural response across species. *PLoS One*. 7:e42440.
- Cuthill IC. 2006. Color perception. In: Hill G, McGraw K, editors. *Bird coloration: mechanisms and measurements*. Cambridge (MA): Harvard University Press. p. 3–40.
- Davies NB. 2000. *Cuckoos, cowbirds and other cheats*. London: T. & A. D. Poyser.
- Dawkins R, Krebs JR. 1979. Arms races between and within species. *Proc R Soc Lond Ser B Biol Sci*. 205:489–511.
- Edvardsen E, Moksnes A, Røskaft E, Øien IJ, Honza M. 2001. Egg mimicry in cuckoos parasitizing four sympatric species of *Acrocephalus* warblers. *Condor*. 103:829–837.
- Endler JA, Mielke PW. 2005. Comparing entire colour patterns as birds see them. *Biol J Linn Soc*. 86:405–431.
- Feeney WE, Langmore NE. 2013. Social learning of a brood parasite by its host. *Biol Lett*. 9. doi:10.1098/rsbl.2013.0443.
- Feeney WE, Medina I, Somveille M, Heinsohn R, Hall ML, Mulder RA, Stein JA, Kilner RM, Langmore NE. 2013. Brood parasitism and the evolution of cooperative breeding in birds. *Science*. 342:1506–1508.
- Feeney WE, Welbergen JA, Langmore NE. 2012. The frontline of avian brood parasite–host coevolution. *Anim Behav*. 84:3–12.
- Gibbs HL, Sorenson MD, Marchetti K, Brooke M de L, Davies NB, Nakamura H. 2000. Genetic evidence for female host-specific races in the common cuckoo. *Nature*. 407:183–186.
- Gloag R, Fiorini V, Reboreda J, Kacelnik A. 2012. Brood parasite eggs enhance egg survivorship in a multiply parasitized host. *Proc R Soc Lond Ser B Biol Sci*. 279:1831–1839.
- Hart NS. 2001. The visual ecology of avian photoreceptors. *Prog Retin Eye Res*. 20:675–703.
- Hart NS, Partridge JC, Cuthill IC, Bennett ATD. 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus* L.) and the black-bird (*Turdus merula* L.). *J Comp Physiol A Sens Neural Behav Physiol*. 186:375–387.
- Higgins PJ, editor. 1999. *Handbook of Australian, New Zealand and Antarctic birds: parrots to dollarbird*. Vol. 4. Melbourne (Australia): Oxford University Press.
- Higgins PJ, Peter JM, editors. 2002. *Handbook of Australian, New Zealand and Antarctic birds: pardalotes to shrike-thrushes*. Vol. 6. Melbourne (Australia): Oxford University Press.
- Higgins PJ, Peter JM, Steele WK, editors. 2001. *Handbook of Australian, New Zealand and Antarctic birds: tyrant-flycatchers to chats*. Vol. 5. Melbourne (Australia): Oxford University Press.

- Joseph L, Wilke T, Alpers D. 2002. Reconciling genetic expectations from host specificity with historical population dynamics in an avian brood parasite, Horsfield's Bronze-Cuckoo *Chalcites basalıs* of Australia. *Mol Ecol*. 11:829–837.
- Kaltz O, Shykoff JA. 1998. Local adaptation in host-parasite systems. *Heredity*. 81:361–370.
- Kilner RM. 2006. The evolution of egg colour and patterning in birds. *Biol Rev Camb Philos Soc*. 81:383–406.
- Kilner RM, Langmore NE. 2011. Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. *Biol Rev Camb Philos Soc*. 86:836–852.
- Langmore NE, Adcock GJ, Kilner RM. 2007. The spatial organization and mating system of Horsfield's bronze-cuckoos, *Chalcites basalıs*. *Anim Behav*. 74:403–412.
- Langmore NE, Cockburn A, Russell AF, Kilner RM. 2009. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behav Ecol*. 20:978–984.
- Langmore NE, Feeney WE, Crowe-Riddell J, Luan H, Louwrens KM, Cockburn A. 2012. Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. *Behav Ecol*. 23:798–805.
- Langmore NE, Hunt S, Kilner RM. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature*. 422:157–160.
- Langmore NE, Kilner RM. 2007. Breeding site and host selection by Horsfield's bronze-cuckoos, *Chalcites basalıs*. *Anim Behav*. 74:995–1004.
- Langmore NE, Kilner RM. 2009. Why do Horsfield's bronze-cuckoo *Chalcites basalıs* eggs mimic those of their hosts? *Behav Ecol Sociobiol*. 63:1127–1131.
- Langmore NE, Kilner RM, Butchart SHM, Maurer G, Davies NB, Cockburn A, Macgregor NA, Peters V, Magrath MJL, Dowling DK. 2005. The evolution of egg rejection by cuckoo hosts in Australia and Europe. *Behav Ecol*. doi:10.1093/beheco/ari041.
- Langmore NE, Maurer G, Adcock GJ, Kilner RM. 2008. Socially acquired host-specific mimicry and the evolution of host races in Horsfield's bronze-cuckoo *Chalcites basalıs*. *Evolution*. 62:1689–1699.
- Langmore NE, Spottiswoode CN. 2012. Visual trickery in avian brood parasites. In: Hughes DP, Brodeur J, Thomas F, editors. *Host manipulation by parasites*. Oxford: Oxford University Press. p. 95–118.
- Langmore NE, Stevens M, Maurer G, Heinsohn R, Hall ML, Peters A, Kilner RM. 2011. Visual mimicry of host nestlings by cuckoos. *Proc R Soc Lond Ser B Biol Sci*. 278. doi: 10.1098/rspb.2010.2391.
- Moksnes A, Røskaft E. 1995. Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *J Zool*. 236:625–648.
- Møller AP, Antonov A, Stokke BG, Fossøy F, Moksnes A, Røskaft E, Takasu F. 2011. Isolation by time and habitat and coexistence of distinct host races of the common cuckoo. *J Evol Biol*. 24:676–684.
- Ödeen A, Håstad O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol Biol Evol*. 20:855–861.
- Ödeen A, Håstad O. 2010. Pollinating birds differ in spectral sensitivity. *J Comp Physiol A*. 196:91–96.
- Ödeen A, Pruett-Jones S, Driskell AC, Armenta JK, Håstad O. 2012. Multiple shifts between violet and ultraviolet vision in a family of passerine birds with associated changes in plumage coloration. *Proc R Soc Lond Ser B Biol Sci*. 279:1269–1276.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2011. *vegan*: community ecology package [cited 2014 January 8]. Available from: <http://cran.r-project.org/web/packages/vegan/index.html>.
- Peer BD, Sealy SG. 2004. Correlates of egg rejection in hosts of the brown-headed cowbird. *Condor*. 106:580–599.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. Vienna (Austria): R Foundation for Statistical Computing.
- Rohwer S, Spaw C. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evol Ecol*. 2:27–36.
- Rothstein SI. 1975. Experimental and teleonomic investigation of avian brood parasitism. *Condor*. 77:250–271.
- Rothstein SI. 1982. Success and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. *Am Zool*. 22:547–560.
- Sato NJ, Mikamf OK, Ueda K. 2010. The egg dilution effect hypothesis: a condition under which parasitic nesting ejection behaviour will evolve. *Ornith Sci*. 9:115–121.
- Sherratt TN. 2002. The evolution of imperfect mimicry. *Behav Ecol*. 13:821–826.
- Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J Exp Biol*. 207:2471–2485.
- Starling M, Heinsohn R, Cockburn A, Langmore NE. 2006. Cryptic genes revealed in pallid cuckoos *Cuculus pallidus* using reflectance spectrophotometry. *Proc R Soc Lond Ser B Biol Sci*. 273:1929–1934.
- Stoddard MC, Prum RO. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *Am Nat*. 171:755–776.
- Stoddard MC, Stevens M. 2010. Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proc R Soc Lond Ser B Biol Sci*. 277:1387–1393.
- Stoddard MC, Stevens M. 2011. Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution*. 65:2004–2013.
- Stokke BG, Moksnes A, Røskaft E. 2002. Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds. *Evolution*. 56:199–205.
- Thompson JN. 1994. *The coevolutionary process*. Chicago (IL): University of Chicago Press.
- Thompson JN. 2005. *The geographic mosaic of coevolution*. Chicago (IL): University of Chicago Press.
- Underwood TJ, Sealy SG. 2006. Grasp-ejection in two small ejectors of cowbird eggs: a test of bill-size constraints and the evolutionary equilibrium hypothesis. *Anim Behav*. 71:409–416.
- Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. *Proc R Soc B Biol Sci*. 265:351–358.
- Zimmerman GM, Goetz H, Mielke PW. 1985. Use of an improved statistical-method for group comparisons to study effects of prairie fire. *Ecology*. 66:606–611.