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RESEARCH ARTICLE

Grey Gerygone hosts are not egg rejecters, but Shining Bronze-Cuckoos lay cryptic eggs

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ABSTRACT

Many brood parasites rely on mimicry to prevent the detection of their eggs by hosts, yet most Australasian cuckoo species lay darkly colored eggs while the eggs of their hosts are pale and speckled. In the dimly lit nests of their hosts, these cuckoo eggs may appear cryptic; however, it is unclear if this disguise has evolved to fool hosts or other cuckoos. Recent work suggests that in at least one species of bronze-cuckoo, cuckoos are more likely to reject conspicuous eggs than are hosts, but it remains unclear whether this is common across the species group. Here, we present field experiments on the sole host of the Shining Bronze-Cuckoo (*Chalcites lucidus lucidus*) in New Zealand, the Grey Gerygone (*Gerygone igata*; known locally as the Grey Warbler), that explored whether this host ignores cuckoo eggs because they are cryptic. Using an avian vision model, we showed that Shining Bronze-Cuckoo eggs were variable in their conspicuousness, but were more cryptic in host nests than the host's eggs. We then experimentally parasitized all available clutches with model eggs that mimicked darkly or brightly colored cuckoo eggs, or were of maximum conspicuousness (white) as determined by visual modeling. Hosts never rejected our model eggs, nor cuckoo eggs when naturally parasitized. Instead, only cuckoos rejected model eggs: In 3 out of 4 experimental nests that were subsequently parasitized, the model egg was taken and replaced by a cuckoo's egg. Together, these data and previous experiments suggest that competition among cuckoos, rather than rejection by hosts, provides a stronger selection pressure for the evolution of cryptic eggs across the genus *Chalcites*.

Keywords: brood parasitism, multiple parasitism, bronze-cuckoo, avian vision, crypsis, evolutionary arms race, egg rejection

Los hospederos de *Gerygone igata* no rechazan sus huevos, pero *Chalcites lucidus lucidus* pone huevos crípticos

RESUMEN

Muchos parásitos de cría imitan los huevos de sus hospederos para prevenir su detección, pero aún así muchas especies de cucos de Australasia ponen huevos de colores oscuros mientras que los huevos de sus hospederos son pálidos y punteados. En los nidos poco iluminados de sus hospederos, estos huevos por lo general son crípticos; sin embargo, no es claro si esto evolucionó para engañar a los hospederos o a otras especies de cucos parásitos. Estudios recientes sugieren que al menos en una especie de *Chalcites* los cucos tienen mayor probabilidad de rechazar los huevos conspicuos que los hospederos, pero aún no es claro si este comportamiento es común a todas las especies del grupo. En este trabajo presentamos experimentos hechos en campo con *Gerygone igata*, el único hospedero de *Chalcites lucidus lucidus* en Nueva Zelanda, para explorar si este hospedero ignora los huevos de los cucos debido a que son crípticos. Usando un modelo de visión aviar, primero demostramos que los huevos de *C. l. lucidus* varían en su conspicuidad pero son más crípticos en los nidos de los hospederos que los propios huevos de los hospederos. Luego introdujimos experimentalmente huevos parásitos en todas las nidadas disponibles con modelos que imitaban huevos de cuco oscuros o brillantes, o de máxima conspicuidad (blancos) de acuerdo a los modelos visuales. Los hospederos nunca rechazaron nuestros modelos ni los huevos de cuco cuando fueron parasitados naturalmente. En cambio, sólo los cucos rechazaron los huevos modelo: en tres de los cuatro nidos experimentales que fueron parasitados posteriormente, el modelo fue rechazado y reemplazado por un huevo de cuco. Estos datos junto con los resultados de experimentos previos sugieren que la competencia entre cucos, y no el rechazo de los hospederos, constituye la presión de selección más fuerte para la evolución de huevos crípticos en el género *Chalcites*.

Palabras clave: carrera armamentista evolutiva, *Chalcites*, crypsis, parasitismo de cría, parasitismo múltiple, rechazo de huevos, visión aviar

INTRODUCTION

To be effective brood parasites, cuckoos must often evolve tricks to fool their hosts (Davies 2011). For example, if hosts are able to recognize and reject cuckoo eggs, cuckoos may evolve eggs that mimic those of their hosts (Soler 2014). However, not all hosts of virulent cuckoos evolve egg rejection behavior (Kilner and Langmore 2011); some hosts seem to ignore a cuckoo's egg even when it is conspicuous against the background of their nest (Aidala et al. 2015) or appears very different from their own eggs (Stoddard and Stevens 2011). Similarly, not all cuckoos have evolved mimetic eggs. For example, in the bronze-cuckoo species group of Australasia and Melanesia (*Chalcites* spp.), many species lay dark olive-green colored eggs while their hosts lay cream-colored eggs with reddish-brown speckles. Darkly colored eggs are rare among birds (Maurer et al. 2011), and this color is a derived trait even within the bronze-cuckoo group (white eggs with speckling is the ancestral egg coloration for *Chrysococcyx* spp. and *Chalcites* spp.; Langmore et al. 2009). Why do these cuckoos lay darkly colored eggs?

The ambient light environment of host nests may provide a clue. All *Chalcites* species that lay dark eggs only parasitize hosts that build domed nests, and these nests are dimly lit (Langmore et al. 2009). When ambient light levels are low, color vision becomes less effective (but see Gomez et al. 2014), so in low light conditions animals are thought to rely more on their perception of brightness (luminance) to detect objects (Vorobyev and Osorio 1998, Osorio et al. 1999, Kelber et al. 2003, Avilés 2008, Lind et al. 2014). Therefore, when birds are attempting to detect eggs in dimly lit environments, the chromatic contrast of eggs against nest backgrounds should be a less useful cue than brightness. For example, Common Nightingales (*Luscinia megarhynchos*), which nest in low light environments, are more discriminating of foreign eggs if these eggs are bright (Antonov et al. 2011). Furthermore, across species, cuckoo hosts that build better illuminated nests are more likely to be egg-rejecters than hosts that build darker nests (Langmore et al. 2005). Ambient light levels also affect the likelihood of egg rejection within species: Eurasian Magpies (*Pica pica*) are more likely to reject cuckoo eggs throughout the season if their nests are well lit (Avilés et al. 2015). Therefore, cuckoo eggs may escape detection by hosts if, given the light environment of host nests, dark coloration suppresses achromatic cues sufficiently to camouflage eggs (Marchant 1972, Langmore et al. 2009).

An additional, or alternative, source of selection for dark cuckoo eggs may come from the cuckoos themselves (Davies and Brooke 1988, Brooker et al. 1990, Langmore et al. 2009, Gloag et al. 2014). Newly hatched chicks of virulent cuckoo species evict host eggs and chicks rapidly (Payne and Payne 1998, Honza et al. 2007), so if a cuckoo

lays her egg in an already parasitized nest (particularly after incubation has begun), it would pay her to remove any previously laid cuckoo eggs (Davies and Brooke 1988). Theoretically, then, cuckoo eggs should be under selection to avoid removal by secondary parasites. This is most likely to evolve when the risk of multiple parasitism is high (Brooker et al. 1990, Langmore et al. 2009) and the selection pressure from hosts is low (Davies and Brooke 1988).

Although there has been little data to support this hypothesis (see Langmore and Kilner 2009), one recent study has demonstrated that the eggs of the Little Bronze-Cuckoo (*Chalcites minutillus*) are indeed dark to escape detection by other cuckoos (Gloag et al. 2014). While hosts (Large-billed Gerygone [*Gerygone magnirostris*]) occasionally rejected eggs that were painted white from their nests, they never removed cuckoo eggs. Cuckoos that parasitized these nests also rarely removed darkly painted eggs, instead removing the conspicuous white eggs. For *C. minutillus*, it appears that competing cuckoos exert a stronger selection pressure on egg color than do hosts. However, uncovering the role that cuckoos, or their hosts, have played in the origin of dark egg coloration requires an understanding of the behavior of more than one *Chalcites* species and its host.

Here, we focus on the Shining Bronze-Cuckoo (*Chalcites lucidus* [previously *Chrysococcyx lucidus*]; known locally as the Shining Cuckoo). This species is thought to have arisen early in the phylogeny of *Chalcites* and is basal to *C. minutillus* (Christidis and Boles 2008). Populations that breed in western and northern Australia (*C. l. plagosus*), New Caledonia (*C. l. layardi*), the Solomon Islands (*C. l. harterti*), and other islands in Melanesia are seen year-round, while those that breed in southern and eastern Australia (*C. l. plagosus*) and throughout New Zealand (*C. l. lucidus*, the nominate form) are thought to overwinter in Melanesia (Erritzøe et al. 2012). It remains unresolved whether these allopatric breeding populations represent subspecies. Their main hosts differ (e.g., thornbills [*Acanthiza* spp.] in Australia and gerygones [*Gerygone* spp.] in New Zealand and Melanesia), and their chicks appear quite different (Gill 1998), but morphological variation among adults is small (Gill 1983a), and there is little genetic differentiation (Sorenson and Payne 2005, Christidis and Boles 2008, Trewick and Gibb 2010). Here we study the New Zealand population and, where necessary, refer to races by their putative subspecies nomenclature.

First, we used an avian vision model to investigate whether Shining Bronze-Cuckoo eggs are cryptic in the nest environment of their sole host in New Zealand, the Grey Gerygone (*Gerygone igata*; known locally as the Grey Warbler). We predicted that, as in other *Chalcites* species (Langmore et al. 2009), cuckoo eggs would match the nest

background more closely than would host eggs, particularly in their luminance (Grey Gerygones build enclosed dome nests similar to those of other *Chalcites* hosts; Gill 1983b). Previous work has suggested that Grey Gerygones rarely reject cuckoo eggs; only 1 clay model egg (out of 11) was ejected from a nest during an artificial parasitism experiment (Briskie 2003), and no eggs have been recorded as being rejected during natural parasitism events (19 nests; Briskie 2003). Furthermore, witnessing a cuckoo in the act of parasitism does not seem to induce hosts to abandon the nest (Briskie 2007). The foreign eggs in these previous observations have all been dark, so a lack of rejection by hosts may have been due to the eggs being too inconspicuous to be detected. Therefore, we created model eggs of the same hue as Shining Bronze-Cuckoo eggs but of different luminance (based on spectral reflectance data). We then experimentally parasitized Grey Gerygone nests to test whether hosts showed rejection defenses if eggs were detectable in the nest (according to their visual system). Direct observations of Shining Bronze-Cuckoos laying their eggs are few (5 nests; Briskie 2007), but a cuckoo was once observed removing a cuckoo egg after laying her own (Briskie 2007). Therefore, if cuckoos were to parasitize our experimental nests, we predicted that our conspicuous model eggs would be more likely to be removed than darker model eggs or host eggs, as in *C. minutillus* (Gloag et al. 2014).

METHODS

Nest Monitoring

We studied parasitism of Grey Gerygones by Shining Bronze-Cuckoos during 2 austral breeding seasons (October–December of 2010 and 2011) in a 240 ha forest fragment near Kaikoura, New Zealand (42.3833°S, 173.6167°E). We searched suitable habitat intensively and followed adults to locate nests; however, many nests that we found were inaccessible or were too advanced for our experiments (already incubating eggs or rearing chicks). We monitored the nests that we could access every 2 days to establish when eggs were laid (Grey Gerygones lay their eggs at 48-hr intervals) and, if parasitized, when parasitism occurred. Shining Bronze-Cuckoos will sometimes lay eggs in nests that are well advanced in incubation, so we continued to monitor nests until hatching. No nests were deserted during incubation in our study, but depredation after hatching (most likely by introduced mammals) was common.

Measuring Egg and Nest Reflectance

To obtain measures of hue and luminance of Shining Bronze-Cuckoo and Grey Gerygone eggs, we used spectrophotometry on eggshells held in museum collections in the UK (Natural History Museum at Tring [NHM]:

$n = 2$ *G. igata*, 1 *C. l. lucidus*) and in New Zealand (Auckland War Memorial Museum [AIM]: $n = 9$ *G. igata*, 11 *C. l. lucidus*; Canterbury Museum [CMNZ]: $n = 6$ *C. l. lucidus*), and, where possible, eggs laid at our field site ($n = 3$ *C. l. lucidus*). It was difficult to safely remove eggs from nests (Gill 1983b), so these latter measurements were taken from shells after eggs had hatched. The collection date (year) was known for all eggs except 6 cuckoo eggs (Shining Bronze-Cuckoo: range = 1879–2010, median = 1951, IQR = 52.5 yr; Grey Gerygone: range = 1889–1991, median = 1904, IQR = 46 yr). Minimal fading of egg coloration occurs in museum collections (Cassey et al. 2010, Hanley et al. 2013), although fading does take place during incubation (Hanley et al. 2016). To be conservative, we repeated analyses of egg conspicuousness without including measurements taken from eggs laid at our field site.

We collected eggshell reflectance measurements using an Ocean Optics (Dunedin, Florida, USA) USB2000 spectrometer connected to a PX-2 xenon pulse light source and an R400-7-UV/VIS reflectance probe that ended in a 45° beveled edge sleeve to maintain a constant distance and angle. Six measurements were taken of each egg, at random locations including the middle and poles, and reflectance was calibrated between every egg against a Spectralon 99% white reflectance standard (Labsphere, Congleton, Cheshire, UK). We used a similar method to measure the color of host nests in the field by taking measurements from 10 random locations within the interior cup of each of 10 nests that we could reach easily with our equipment. Nests are lined with gray feathers (Gill 1983b), and spectral measurements among and between nests did not vary greatly (Figure 1). Over 2 consecutive sunny days we also measured irradiance ('ambient light') by taking 5 measurements at different angles within these 10 nests using a cosine-corrected spectrometer and 600 × 2 probe (Ocean Optics; spectrometer set to an integration time of 5,000). Means of these measurements were used for later analyses (Figure 1).

Visual Modeling of Egg Coloration

We quantified how cryptic Shining Bronze-Cuckoo eggs were in Grey Gerygone host nests by following very similar methods to Langmore et al. (2009). Using pavo (Maia et al. 2013), a package implemented in R 3.3.0 (R Core Team 2016), we measured the color and luminance from reflectance spectra of eggs and nests using avian visual processing models (Vorobyev et al. 1998, Hart 2001) that incorporated our measurements of average ambient light. The average spectrum for each egg or nest was used in these models to calculate the quantum catches for the 4 photoreceptor cones thought to be responsible for color vision in birds and the double cone thought to be

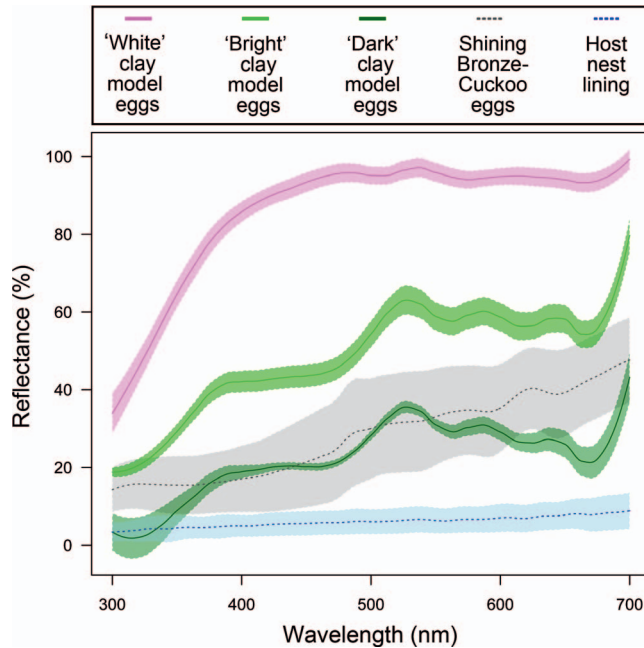


FIGURE 1. Reflectance spectra of 3 types of clay model egg ($n = 5$ for each) used in experiments exploring whether Grey Gerygones (*Gerygone igata*) ignore cuckoo eggs because they are cryptic, compared with variation in Shining Bronze-Cuckoo (*Chalcites lucidus lucidus*) eggs ($n = 18$) held in museum collections. Spectra collected from 10 Grey Gerygone nests (means of 10 measurements each) are also shown. Mean spectra are shown with lines and the shaded area for each shows the standard error.

responsible for achromatic (luminance) perception. The exact visual sensitivities of Shining Bronze-Cuckoos and Grey Gerygones are not known; however, opsin gene expression (Aidala et al. 2012) suggests that the peak sensitivity of the cones that detect ultraviolet wavelengths is close to the visible spectrum (known as VS). Therefore, we used the known cone sensitivities for another VS species, the Indian Peafowl (*Pavo cristatus*), in our visual models. Previous studies have rarely found meaningful differences in results when the peak sensitivity used has differed (e.g., Langmore et al. 2009) and, when we repeated our analyses using the visual sensitivities of the ultraviolet-sensitive (UVS) Eurasian Blue Tit (*Cyanistes caeruleus*), our results also did not differ (results not shown).

Next, we used the quantum catches to model color and luminance discrimination between cuckoo and host eggs, and to model how distinctive each was from the nest lining. All host species used by Shining Bronze-Cuckoo races build enclosed nests, and it is not clear exactly how dim ambient light affects avian visual discrimination (Gomez et al. 2014). Dim light may increase neural and receptor noise, thus making discrimination more difficult, or dim light might not hinder discrimination at all as there may be physiological mechanisms that minimize these

difficulties (Osorio et al. 2004). Therefore, we ran each visual model twice, once taking into account both sources of noise to simulate limited discrimination ability (Q), and once including only neural noise to simulate ideal discrimination (N). Both methods produced qualitatively similar results, so we present the results based on ideal discrimination (N).

Different receptor cones are used for chromatic and achromatic discrimination tasks, however birds probably integrate information from each in their behavioral responses (e.g., Spottiswoode and Stevens 2010), even in dim lighting (Gomez et al. 2014). Therefore, instead of investigating color and luminance separately (Langmore et al. 2009), we first calculated the contrast between egg and nest relative to variation in the nest background by calculating the average perceptual distance between eggs with each measurement of nest color (ΔS) or luminance (ΔL) following equation 3 of Håstad et al. (2005). 'Just Noticeable Differences' (JNDs) are a commonly used method for quantifying contrasts between objects, but JNDs imply perceptual thresholds that are poorly understood for many avian species, even under bright light conditions (Olsson et al. 2015). Therefore, second, we used the contrasts to evaluate total egg conspicuousness (E_N). Following Endler and Mielke (2005) and Darst et al. (2010), we calculated the Euclidean distance between pairs of contrasts using $E_N = (\Delta S^2 + \Delta L^2)^{0.5}$. As both contrasts were expressed relative to the same backgrounds, this produced a vector in 'perceptual space' (Darst et al. 2010), with increasing values indicating greater conspicuousness. These data were not normally distributed, so we used Kruskal-Wallis nonparametric tests to determine whether host or cuckoo eggs differed in conspicuousness against the lining of the host's nest, and a Breusch-Pagan test (using the car package; Fox and Weisberg 2011) to assess homoscedasticity as this test does not rely on assumptions of normality.

Experimental Parasitism

Model eggs were made by shaping white modeling clay (FIMOair, Staedtler, Nuremberg, Germany) around a weighted wooden bead. The modeling clay was then air-dried, so that the model eggs mimicked Shining Bronze-Cuckoo eggs in size (model eggs: $\bar{x} = 18.54 \times 12.61$ mm, $SD = 0.63 \times 0.27$ mm, $n = 10$; Shining Bronze-Cuckoo eggs: $\bar{x} = 18.68 \times 12.63$ mm, $n = 4$ [from Gill 1983c, SD not given]) and mass (model eggs: $\bar{x} = 1.84$ g, $SD = 0.10$ g; Shining Bronze-Cuckoo eggs: $\bar{x} = 1.85$ g, $SD = 0.06$ g [from Gill 1983c]). The clay that we used reflected both human-visible and ultraviolet light wavelengths (Figure 1). Each nest received 1 of 3 model eggs that varied in its luminance: (1) mimetic to dark Shining Bronze-Cuckoo eggs ('dark'; see Results), (2) mimetic to bright Shining Bronze-Cuckoo eggs ('bright'), or (3) highly conspicuous

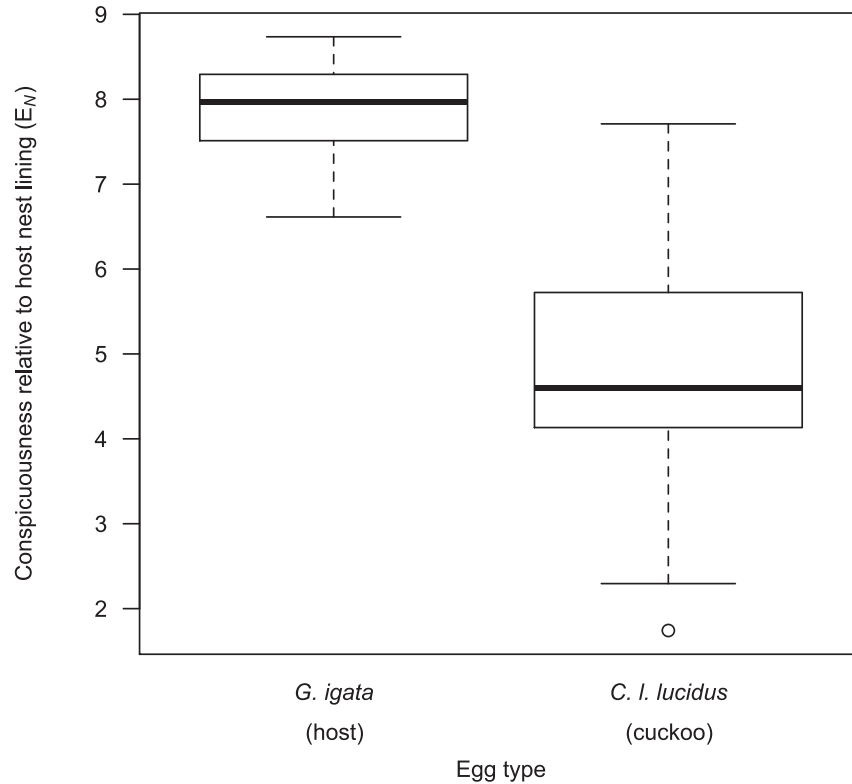


FIGURE 2. Host eggs (*Gerygone igata*; $n = 11$) were more conspicuous overall against the nest lining ($n = 10$) than Shining Bronze-Cuckoo (*Chalcites lucidus lucidus*; $n = 21$) eggs (Kruskal-Wallis: $\chi^2 = 18.88$, $P < 0.001$). Conspicuousness was modeled conservatively by assuming that dim light did not affect discrimination (E_N). Heavy lines show the median values and boxes the interquartile range; whiskers are 1.5 times the interquartile range, and circles are outliers.

against the nest background and reflected maximum light ('white'). We manipulated luminance (Kruskal-Wallis test: $\chi^2 = 19.03$, $P < 0.001$), but not maximum chroma ($\chi^2 = 3.46$, $P = 0.18$), of the dark and bright model eggs by applying layers of ink using a Copic marker pen (Too Corporation, Tokyo, Japan) in the shade 'green gray' BG-93: Dark model eggs were colored with 3 layers of ink, and bright model eggs were colored with 1 layer.

When nests were found before clutch completion (20 nests), we inserted 1 model egg after at least 1 egg had been laid, and when parents were not present (to avoid interfering with the behavior of hosts; Hanley et al. 2015). None of the hosts were color banded, but as Grey Gerygones are territorial (Gill 1982), and we performed our experiments across the study site, to the best of our knowledge we avoided artificially parasitizing second nesting attempts of the same pairs. We considered model eggs to have been accepted by hosts if they remained in the nest for 6 days following the onset of incubation and were warm when checked (following Briskie 2003). Model eggs in nests that were later naturally parasitized were scored as 'accepted' if the host clutch was reduced but the model egg remained, or were scored as 'rejected' if the model egg was missing but the size of the host's clutch remained the same

(following Gloag et al. 2014). Clay eggs were air dried, but could still easily be scratched by us. Therefore, at hatching, we checked model eggs for scratch marks which might have indicated unsuccessful rejection attempts by hosts, but none were seen.

RESULTS

Visual Modeling of Egg Coloration

As predicted, Grey Gerygone host eggs were more similar in color to the nest lining than Shining Bronze-Cuckoo eggs (ΔS ; median: host = 0.32, cuckoo = 1.17; range: host = 0.14–0.37, cuckoo = 0.03–4.86). The lower luminance of cuckoo eggs (ΔL ; median: host = 7.96, cuckoo = 4.25; range: host = 6.61–8.73, cuckoo = 1.61–7.71), however, meant that cuckoo eggs were less conspicuous overall than host eggs (Figure 2). Chromatic and achromatic measurements of the 3 cuckoo eggs collected in the field were within 1.5 times the interquartile range of eggs measured from museum collections, although eggs collected in the field were less conspicuous overall (range of E_N ; field eggs: 1.74–2.78, museum eggs: 2.85–7.71). Regardless, host eggs remained more conspicuous than cuckoo eggs when cuckoo eggs collected in the field were removed from

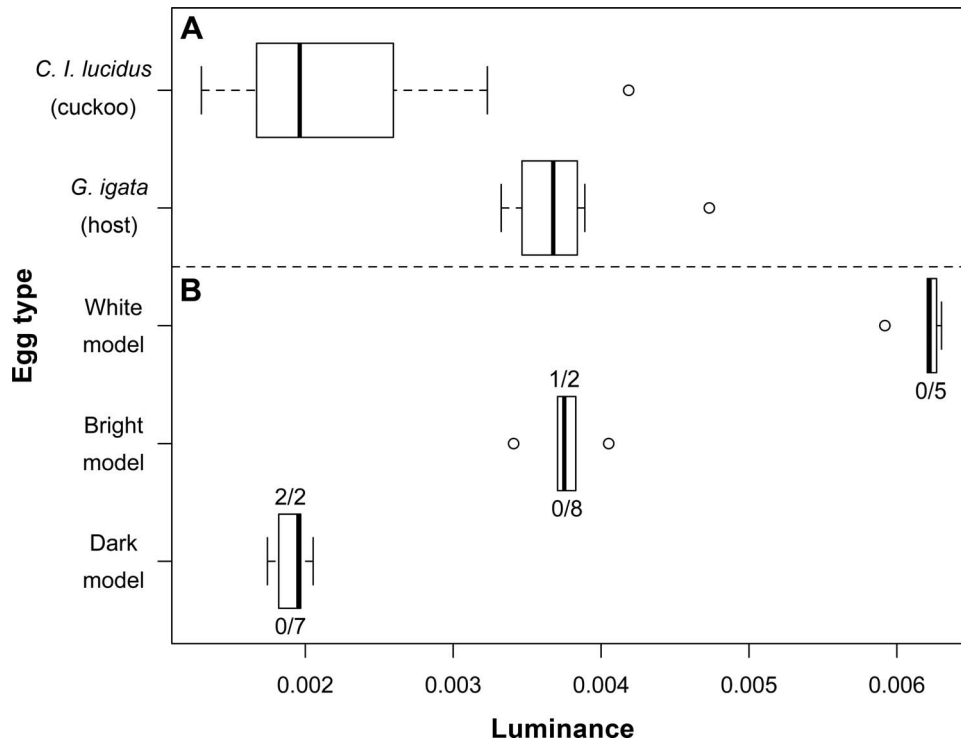


FIGURE 3. Luminance ('brightness') of (A) Shining Bronze-Cuckoo (*Chalcites lucidus lucidus*) and host (Grey Gerygone [*Gerygone igata*]) eggs, and (B) model eggs used in artificial parasitism experiments. As in Figure 2, heavy lines show the median values and boxes the interquartile range, while whiskers are 1.5 times the interquartile range; values beyond this are shown as open circles. Numbers above boxes in panel B indicate the number of model eggs removed by cuckoos, and numbers below boxes show that hosts removed no model eggs. Nests containing 'white' model eggs were not naturally parasitized.

analysis (Kruskal-Wallis: $\chi^2 = 17.47$, $P < 0.001$). Therefore, although cuckoo eggs tended to vary more than host eggs (Breusch-Pagan test, complete dataset: $\chi^2 = 5.21$, $P = 0.02$; with field eggs removed: $\chi^2 = 3.98$, $P = 0.05$), in the dark nest environment of this host, Shining Bronze-Cuckoo eggs should have been more difficult to detect than host eggs.

Who Selects for Crypsis?

We successfully manipulated the luminance of 'bright' and 'white' model eggs compared with 'dark' model eggs and Shining Bronze-Cuckoo eggs by a factor of 2 (Figure 3). Only the luminance of 'dark' model eggs was similar to that of cuckoo eggs (Wilcoxon signed-rank tests compared with cuckoo eggs; 'dark': $W = 44$, $P = 0.78$; 'bright': $W = 5$, $P = 0.002$; 'white': $W = 0$, $P < 0.001$). Despite the conspicuousness of the eggs, however, Grey Gerygones rejected none of the model eggs (Figure 3), nor did they remove cuckoo eggs from naturally parasitized nests (2010: 9/21 nests parasitized; 2011: 5/20 nests parasitized). In contrast, cuckoos later parasitized 4 nests containing model eggs (all in 2010), and at 3 of these the model egg was removed instead of a host egg (Figure 3). Clutch sizes (host eggs plus model eggs) varied among these nests: 2

nests contained 3 eggs, 1 nest contained 4 eggs, and the fourth nest contained 5 eggs. A host egg was taken instead of a model egg from one 3-egg clutch. Therefore, the probability of our 3 model eggs being taken instead of a host egg ($1/3 \times 1/4 \times 1/5$) was just $P = 0.017$. Too few nests were parasitized to test differences among model egg types statistically, but, regardless of type, parasitized nests were more likely to lose a model egg than unparasitized nests (Fisher's exact test, $P = 0.02$).

DISCUSSION

Our visual modeling results showed that Shining Bronze-Cuckoo eggs, similarly to the eggs of other cuckoos in the genus *Chalcites* (Langmore et al. 2009), were less conspicuous in the dim nest environment of their host than the Grey Gerygones' own eggs. However, our experiments suggest that reduced conspicuousness is unlikely to be an adaptation to prevent egg rejection by hosts; none of the Grey Gerygones rejected foreign eggs, even when they were visually conspicuous in the nest environment. This confirms the results of previous experiments (Briskie 2003) and observations (Gill 1983c), wherein Grey Gerygones accepted darkly colored eggs. In

contrast, as in recent work with a congeneric cuckoo (Gloag et al. 2014), Shining Bronze-Cuckoos in our study were able to discriminate foreign eggs from host eggs. Only cuckoos removed model eggs from nests included in our experiments. Our sample size was small, so we cannot rule out the possibility that hosts might occasionally reject cuckoo eggs and influence egg phenotype. However, our results suggest that egg removal by cuckoos is likely to be the stronger selection pressure shaping the evolution of dark cuckoo eggs.

Why did hosts not reject foreign eggs when they were made conspicuous? It is possible that by using clay eggs we missed attempts to reject eggs (Martín-Vivaldi et al. 2002, Antonov et al. 2009; but see Prather et al. 2007), or that the model eggs were not convincing enough stimuli (Lahti 2015). However, these explanations seem unlikely as a Grey Gerygone was recorded rejecting a similar clay model egg (painted dark) in a previous experiment (1 out of 11 nests; Briskie 2003), and hosts with a similar bill size to Grey Gerygones (Gill 1980) have also occasionally rejected similar model eggs (Briskie 2003). It is possible that Grey Gerygones may need more information about the threat of parasitism to take the risk of evicting an egg from the nest (Thorogood and Davies 2016). This also seems unlikely, however, as Grey Gerygones do not abandon their nests even when they are present during the act of parasitism (0 rejections out of 2 parasitism events; Briskie 2007).

Alternatively, the dark coloration of cuckoo eggs may have prevented Grey Gerygones from evolving egg rejection defenses. As darkly colored eggs are common throughout the *Chalcites* clade (Langmore et al. 2009), it is possible that initial parasitism of Grey Gerygones was by cuckoos that already laid inconspicuous eggs (Brooker and Brooker 1989, Brooker et al. 1990). However, we found that some Shining Bronze-Cuckoo eggs were as conspicuous as host eggs when viewed against the nest lining (Figure 3). Furthermore, in the only other study investigating selection for dark *Chalcites* eggs (Gloag et al. 2014), the host (*Gerygone magnirostris*, a congener of the Grey Gerygone) showed some egg rejection (4 out of 23 pairs [17%] rejected model eggs, including those with a similar luminance to cuckoo eggs). As Grey Gerygones and Shining Bronze-Cuckoos are likely to have been in contact for more than 10,000 yr (Gill 1998), this suggests either that selection pressure on Grey Gerygones to evolve rejection must be constrained by other factors, or that conspicuous eggs are encountered too infrequently for rejection to spread throughout the population (Grim 2006).

Given that our visual modeling suggested that Grey Gerygones should be able to see the most conspicuous foreign eggs, perhaps 'ignoring' these eggs provides a benefit to hosts (Gloag et al. 2012). If cuckoos preferentially remove cuckoo eggs rather than host eggs (Gloag et

al. 2014), then more host eggs will survive any subsequent parasitism events. A dilution effect such as this would be especially beneficial for Grey Gerygones as cuckoos often lay their eggs late in the host's incubation period and, if these eggs hatch, the cuckoo sometimes fails to remove host young (Gill 1983c). This dilution effect would become even more valuable if hosts discriminate against cuckoo chicks after hatching (Sato et al. 2010a), and chick rejection may be more likely to evolve if hosts show weak defenses at earlier stages (Langmore et al. 2003, Grim 2006, Yang et al. 2015). Other *Gerygone* species reject *Chalcites* cuckoo chicks but not eggs (Sato et al. 2010b, 2015, Tokue and Ueda 2010), so perhaps Grey Gerygones might also show chick discrimination (Gill 1998, Grim 2011). This deserves further study.

Why are Shining Bronze-Cuckoo eggs variable in their conspicuousness? There are several possible explanations. First, cuckoo egg color may covary with nest location. Grey Gerygones build similarly sized and shaped nests, but these are built from 0.5 m to 17 m above the ground (Gill 1982). If light conditions are variable among nest sites, cuckoo egg color may have diversified to match these light environments to optimize the crypsis of eggs and avoid detection (Avilés et al. 2015).

Second, there may be variation in cuckoo egg color if selection pressure is weak. Since 1976, multiple cuckoo eggs have been observed in only ~2% of parasitized Grey Gerygone nests in our field site (0/24 nests: Gill 1983c; 0/19 nests: Briskie 2003; 2/5 nests: Briskie 2007; 0/41 nests, this study), and have never been reported in records collected across New Zealand (0/17 Ornithological Society of New Zealand [OSNZ] nest record cards; M.G. Anderson personal communication). This suggests that competition for host nests is weak, and that cuckoos rarely encounter eggs laid by conspecifics. Shining Bronze-Cuckoos in Australia (*C. l. plagosus*) experience greater competition for host nests (~8% of 870 parasitized nests had multiple cuckoo eggs; Brooker and Brooker 1989) and, anecdotally at least, variation in egg color is less than the variation that we detected here (R. M. Kilner personal observation). It has been suggested that pigmentation levels are optimized to enhance embryo fitness (Lahti and Ardia 2016). As dark eggshells can slow embryonic development (Maurer et al. 2014), olive-green pigmentation could be costly for Shining Bronze-Cuckoos as hatching first facilitates the removal of competition (Gill 1998). If the benefit of crypsis is lower than this putative cost of dark coloration, then variability in egg color could result. Shining Bronze-Cuckoos also breed on many islands in Melanesia, with varying degrees of competition for hosts (Erritzøe et al. 2012). An ideal next step would be to compare multiple parasitism rates, egg removal behavior by cuckoos, and egg color variation among these populations, as well as among different *Chalcites* species.

Our visual modeling suggested that Shining Bronze-Cuckoo eggs are cryptic, in that they are less conspicuous than host eggs against the nest lining (Langmore et al. 2009). However, inconspicuous coloration is only cryptic if it leads to a reduced risk of detection (Stevens and Merilaita 2009). Despite the 'dark' eggs in our experiment being similar in luminance to real cuckoo eggs, cuckoos removed both these and the 'bright' model eggs that were twice as luminous. As only 4 experimental nests were parasitized, however, the data are too few to conclude whether or not dark eggs are cryptic. Furthermore, the coloration of the 'dark' model eggs that we used was based on the average luminance of Shining Bronze-Cuckoo eggs. As discussed, these eggs are highly variable but rarely encountered, so a less conspicuous cuckoo egg may still avoid detection. Most importantly, our study shows that cuckoos are much more likely than hosts to eject foreign eggs from nests. Combined with previous studies, both on Grey Gerygones (Gill 1983c, Briskie 2003, 2007) and on a congeneric host and cuckoo (Gloag et al. 2014), our results therefore suggest that the dark coloration of Shining Bronze-Cuckoo eggs is more likely to be an adaptation in response to selection pressure from cuckoos than from their hosts.

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