Eggshell conspicuousness in ground nesting birds: do conspicuous eggshells signal nest location to conspecifics?

Daniel Hanley[a,b]*, **Mary Caswell Stoddard[c,d], Phillip Cassey[e] and Patricia L. R. Brennan[f]**

[a]*Department of Integrative Biology, University of Guelph, Ontario, N1G 2W1, Canada*
[b]*Department of Zoology and Laboratory of Ornithology, Palacký University, Olomouc, 771 46, Czech Republic*
[c]*Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology and Harvard University, Cambridge, MA 02138, USA*
[d]*Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK*
[e]*Earth and Environmental Sciences, University of Adelaide, Adelaide, 5005, Australia*
[f]*Biology Department, University of Massachusetts, Amherst, MA 01003, USA*
E-mail: dhanley@uoguelph.ca

ABSTRACT

Predators can adversely impact nesting success and therefore the presence of seemingly conspicuous eggshells would appear maladaptive. The ratites, especially the tinamous, exhibit a diverse array of eggshell colours that appear to differ strikingly from their nesting substrate, while most ground-nesting species that do not build a nest lay camouflaged eggs. Surprisingly, there is little research on how these nest contents appear to ecologically-relevant viewers, including conspecifics and predators. Here we use visual modelling to compare eggshell conspicuousness in two distinct avian lineages differing in eggshell colour and breeding biology: ratites and galliformes. Ratites generally lay vibrant, unspeckled eggs directly on the ground, while galliformes tend to lay subtler, speckled eggs on nests built on the ground. We test the hypothesis that eggshell colours in ratites are more conspicuous, from the perspective of an avian conspecific, than those of galliformes. We found that the uniform colour covering the surface of the eggshell colour (hereafter, eggshell background colour) differs noticeably from the nesting substrate in both ratites and galliformes. However, the speckling pattern of galliform eggs often masks their conspicuous eggshell background colour, which contributes to a less conspicuous appearance overall. We tested the hypothesis that eggshell conspicuousness in ratites serves an intraspecific signalling function to advertise nest location to females in communally nesting species. We found no support for this hypothesis, suggesting that selection pressure for communal laying did not result in the diversity of conspicuousness found in avian eggs. Overall, we argue that future investigations of egg coloration should consider egg appearance (eggshell background colour and speckling) in the context of the natural nest substrate, all from the perspective of the relevant visual receiver.

Keywords: avian visual modelling, conspicuousness, egg colour, galliformes, ratites, tetrahedral colour space, tinamou

1. INTRODUCTION

The egg is arguably the most critical life stage for a bird (Wallace, 1871). Defences afforded to birds' eggs include their natural camouflage and parental defence. Despite this, many species lay strikingly conspicuous eggshells that seem counterintuitive considering the predation risk facing eggs (Götmark, 1992; Blanco et al., 2002; Svagelj et al., 2003; Avilés et al., 2006; Castilla et al., 2007; Westmoreland, 2008). Over the past 200 years, researchers have been interested in why birds lay eggs that are conspicuous despite threats posed by visually oriented predators (reviewed in Stoddard et al., 2011a). Hypotheses include inter- and intra-specific signalling (Moreno et al., 2003; Hanley et al., 2010), selection by environmental factors (McAldowie, 1886; Maurer et al., 2011), and tradeoffs between these competing selection mechanisms (Magige et al., 2008). However, much of the underlying theory behind these hypotheses has been driven by how eggs appear to the human eye, sometimes within a natural history collection outside the contexts of the nest and nesting environment.

Due to the advances in avian visual modelling and portable spectrophotometers suitable for the field, ecologists have begun to consider colour perception from the perspective of the intended viewer (Bennett et al., 1994; Kelber et al., 2003; Endler et al., 2005b). Therefore, birds' eggs should be studied from the perspective of the relevant signal receiver, which is usually a conspecific or a predator. In birds, colour vision arises from four single cone-types, with peak sensitivities to longwave (*l*), mediumwave (*m*), shortwave (*s*), and ultraviolet (*uv*) or violet (*v*) light (reviewed in, Cuthill, 2006), while luminance (*i.e.* brightness) discrimination is thought to be controlled by double cones (Jones et al., 2004).

Of all ground-nesting birds, tinamous (Family Tinamidae) exhibit the most dramatic eggshell conspicuousness (Figure 1; Walters, 1994, 2006; Davies, 2002) and do not build a concealed nest (Davies, 2002; Brennan, 2010). Their eggs are easily seen from a distance by a human observer if the male is not incubating (Skutch 1960, Brennan 2010). The role of these strikingly conspicuous eggshells has been questioned by numerous observers of avian behaviour because the presence of conspicuous eggs laid directly on the ground seems counterintuitive (Lancaster, 1964; Weeks, 1973; Schwartz et al., 1984; Davies, 2002; Brennan, 2009, 2010). Males provide all the incubation and parental care in this group, and male tinamous are highly attentive incubators, covering the eggs up to 98% of the time (Brennan, 2009).

Therefore, it is not surprising that recent research suggests that the predators of great tinamous (*Tinamus major*) appear to locate clutches by using cues from incubating males rather than visual detection of the eggs (Brennan, 2010). If most predators use non-visual cues to locate nests or if male incubation effectively reduces the cost of conspicuous egg colours, egg colouration may be freed from predation pressures and available to serve an intraspecific signalling function (Brennan, 2010).

A possible explanation for this conspicuous colouration is that tinamous use vibrant egg colouration as an intraspecific signal of nest location between laying females (Weeks, 1973; Schwartz et al., 1984; Brennan, 2010). This hypothesis can be extended to ratites in general because the mating system of most ratites is characterised by exclusive male parental care and communal nesting (Handford et al., 1985). Communal clutches are beneficial to ratites because partial predation is common, and eggs in larger clutches have significantly higher survival probability than eggs in smaller clutches (Bertram et al., 1981; Fernandez et al., 1998, 2000; Brennan, 2010). Moreover, females cannot quickly lay all the eggs that a single male can incubate (Vehrencamp et al., 2004) and therefore eggshell conspicuousness as an advertisement of nest location could be adaptive to insure quick completion of a sufficiently large clutch. While some ratites initiate incubation prior to clutch completion, these large clutches are often left exposed for extended
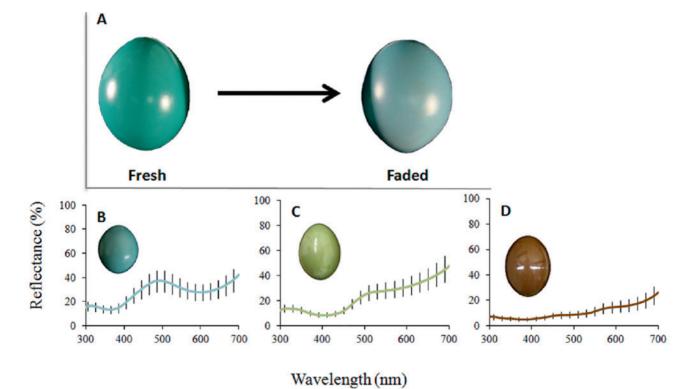

Figure 1 The coloration of *Tinamus major* eggshells fades rapidly during the laying period, (A) even over the course of one week (depicted here). We illustrate some of the diversity in tinamou eggshell colouration by presenting a photograph and a reflectance spectrum for the eggshells of B) *Tinamus major*, C) *Eudromia elegans*, D) and *Nothura boraquira* measured in a natural history collection.

periods, and full incubation does not occur until the clutch is complete (Cabot, 1992; Folch, 1992a, 1992b, 1992c, 1992d, 1992e; Brennan, 2010). This provides a variable interval during the laying and early incubation period that may allow for signalling to occur just prior to clutch completion and steady incubation.

In this paper, we examine the visual conspicuousness, from the perspective of a bird's eye, of eggs in two avian groups to determine if the eggs of ground-nesting species are conspicuous to conspecifics. Although there is a growing body of literature on eggshell colouration, there is relatively little known about how conspicuous eggs are relative to their natural nests. Here we use receptor noise-limited visual modelling (Vorobyev *et al.*, 1998a, 1998b) and tetrahedral colour space modelling (Goldsmith, 1990; Stoddard *et al.*, 2008) to examine eggshell background colour conspicuousness, relative to nesting substrate, in ratites and galliformes. Unlike ratites, galliformes lay eggs with a subtle eggshell background colour and speckling pattern that reduces their conspicuousness (Harrison, 1975; Baicich *et al.*, 1997). We compare the degree of conspicuousness between these two ground nesting groups and expect that ratites lay more conspicuous eggs than galliformes. Here we use this comparison to establish a context for the conspicuousness values of the ratite eggs, allowing us to evaluate how conspicuous ratite eggs are relative to another group of birds, rather than examining conspicuousness values in isolation. Then we examine whether communal nesting is associated with eggshell conspicuousness in ratites. If conspicuous egg colouration is used as a female–female signal of nest location, we expect that eggshell conspicuousness will be higher in communally nesting species. In contrast, most galliformes lay a large clutch quickly and females incubate alone (Baicich *et al.*, 1997). Therefore, we do not test the conspecific signalling hypothesis in galliformes.

2. METHODS

2.1 Egg colour assessment

We measured the colouration of 430 eggshell samples from 26 ratites and 15 galliformes stored in four natural history collections: American Museum of Natural History, New York, USA, Field Museum of Natural History, Chicago, USA, the University Museum of Zoology, Cambridge, UK and the Natural History Museum, Tring, UK. We used a reflectance spectrometer (USB4000, Ocean Optics, Dunedin, Florida, USA) with a portable full spectrum light source (PX-2 pulsed xenon, Ocean Optics, Florida, USA) and Spectralon white standard (WS-1-SL, Spectralon, Florida, USA) to measure egg colouration across the entire avian visual range (300–700 nm, Jacobs, 1992; Maier, 1993; Maier *et al.*, 1993; Bowmaker *et al.*, 1997; Hart, 2001b). At the National History Museum at Tring we used an Ocean Optics USB 2000 spectrometer and a DT mini light source, with a coincident

normal measurement angle (Cassey *et al.*, 2010b). We found that these differences in protocol did not result in consistent differences in colour measurements (*unpublished data*). We measured each egg six times, with two measurements each on the blunt end, equator, and the pointed end. We collected 10 potential background substrates from Ojibway Park, Windsor, ON (42°15'53.09"N, 83° 4'30.58"W) and measured each of these ten times. The background substrates measured included light and dark sand, light and dark dried leaf litter, woodland litter, green and dried grasses, as well as a sample containing both grasses and twigs. These backgrounds include all those used by ratites to lay their eggs (Davies, 2002). We used life history accounts for each species to choose the mean background substrate reflectance spectra that would best represent the natural nesting material used by these species.

All spectra were smoothed with a locally-weighted polynomial regression using the *lowess* function implemented in the statistical package R (R Development Core Team, 2010). We averaged all egg measurements to obtain one spectrum for each. We also averaged our values for each background substrate because the purpose of these reflectance curves was to provide a generic spectrum describing a particular substrate type. After averaging, each average spectrum was visually inspected prior to analyses. For statistical analyses, we applied a three point scoring system to quantify the extent of eggshell speckling (Kilner, 2006), such that 0 indicates eggs with no speckles, 1 indicates eggs with some speckling but clearly visible eggshell background colouration, and 2 represents eggs with widespread eggshell speckling covering most of the eggshell surface.

2.2 Modelling egg colour using a receptor noise-limited visual model

The conspicuousness of an object is dependent on the visual capabilities of the viewer, the reflectance of the object, the reflectance of the background upon which the object is viewed, and the ambient light characteristics (Endler, 1990; Kelber *et al.*, 2003). We used a receptor noise-limited opponent model to determine the conspicuousness of the eggs of ratites and galliformes when laid on various substrates. These models incorporate normalised spectral sensitivity, a daylight irradiance spectrum, and our measurements of egg reflectance (Endler, 1993; Vorobyev *et al.*, 1998a), and should estimate discriminability for eggs when viewed by a conspecific or species with a similar visual system.

Colour vision can be represented by an *n*-dimensional colour space, where *n* refers to the number of cone types in the viewer (Vorobyev, 2003) and the axes are maximum quantum catches for each cone type. Diurnal birds are tetrachromatic, possessing four photopigments that vary in wavelengths of maximum sensitivity. Bird species possess either an ultraviolet sensitive (UVS) cone type or a violet

sensitive (VS) cone type (Bowmaker *et al.*, 1997; Hart *et al.*, 2000). Recent research has provided strong evidence that all ratites, including ostriches and rheas, possess the UVS cone type (Wright *et al.*, 2001; but see, Ödeen *et al.*, 2003; Aidala *et al.*, 2012). Therefore we use the generic cone sensitivity data for UVS avian vision provided by Endler and Mielke (2005a). We use cone sensitivity data from the Domestic Fowl (*Gallus gallus domesticus*) as a representative for galliformes, which have VS cone types (Govardovskii *et al.*, 1977; Partridge, 1989; Bowmaker *et al.*, 1997; Hadfield, 2004). Quantum catch is calculated as

$$Q_i = \frac{\int_\lambda R_i(\lambda)S(\lambda)I(\lambda)d\lambda}{\int_\lambda R_i(\lambda)} \tag{1}$$

where R_i represents the spectral sensitivity of cone type *i*, *S* represents the spectral reflectance of the object, and *I* represents the normalised irradiance spectrum. Here we used normalised irradiance spectra available in SPEC (Hadfield, 2004) representing average daylight conditions as well as filtered forest ambient light (Endler, 1993). We calculated receptor noise with a flexible function accounting for the inherent noise to signal ratio for all cone types relative to the proportion of receptor types in the eye (Vorobyev *et al.*, 1998b; Vorobyev, 2003; Cheney *et al.*, 2009) as

$$e_i = \sqrt{\frac{(1/(\log(T\frac{(Q_{i,a}+Q_{i,b})}{2}))^2 + w_i^2)}{n_i}} \tag{2}$$

where T is a scaling factor for luminance level (set to 10,000), w_i is the Weber fraction accounting for differences in response sizes based on magnitude of stimuli (Wyszceki *et al.*, 1982) (set to 0.05 for all cone types), n_i represents the relative number of receptor cells for each receptor type. The relative proportion of receptor types for UV, shortwave, medium-wave, and long sensitive cone types vary according to the ecology and behaviour of the organism (Hart, 2001a). Without specific information on the relative proportion of receptor types, we used the photoreceptor abundance ratios for ground feeding omnivorous birds as our best estimate for this group. Specifically, we used 9.4:14.05:17.3:15.95 as the relative proportion of receptor types for ratites, which represents the average relative cone abundance for Peafowl (*Pavo cristatus*) and Spotted Dove (*Streptopelia chinensis*), which clustered together as two species with a similar distribution of cones and that had similar feeding strategies (Hart, 2001a). We used 7.4:13.9:16.3:15.6 for galliformes, which represents the relative cone abundance for the peafowl (VS, SWS, MWS, LWS) (Hart, 2001a).

We incorporate receptor noise within our estimate of distance between colours within this colour space, or

discriminability, with the following function (Vorobyev *et al.*, 1998a):

$$(\Delta S)^2 = \frac{\left[\begin{array}{l}(e_1^2 e_2^2)(\Delta f_4 - \Delta f_3)^2 + (e_1^2 e_3^2)(\Delta f_4 - \Delta f_2)^2 + (e_1^2 e_4^2)(\Delta f_3 - \Delta f_2)^2 + \\ (e_2^2 e_4^2)(\Delta f_3 - \Delta f_1)^2 + (e_3^2 e_4^2)(\Delta f_2 - \Delta f_1)^2 + (e_3^2 e_2^2)(\Delta f_1 - \Delta f_4)^2 \end{array}\right]}{(e_1 e_2 e_3)^2 + (e_1 e_2 e_4)^2 + (e_1 e_3 e_4)^2 + (e_2 e_3 e_4)^2} \tag{3}$$

where Δf_i is the difference in the logarithm of quantum catch between two stimuli (Vorobyev *et al.*, 1998a). Discriminability estimates calculated in this way represent units of just noticeable differences, where a value of one represents a discriminable difference between two colours irrespective of brightness differences. We calculated quantum catch and discriminability using the program SPEC (Hadfield, 2004) in the statistical package R (R Development Core Team, 2010) assuming average daylight and filtered forest light conditions (Endler, 1993). For each species we chose an ecologically relevant nesting substrate, and then compared eggshell reflectance spectra to one average nesting substrate per species. To estimate luminance contrast we ran similar models with double cone sensitivity using data from the Blue Tit (*Cyanistes caeruleus*) as an estimate for a UVS species and for the Domestic Fowl as an estimate of a VS species (available in SPEC). As birds possess a single double cone (Wright *et al.*, 2001; Hunt *et al.*, 2009), the relative abundance of receptor cells was ignored in these models. We calculated achromatic discrimination as, $\Delta L = |\Delta f_i / w|$ (*sensu*, Siddiqi *et al.*), where *w* was set to 0.05 and where

$$\Delta f_i = \ln(qi) - \ln(qj) \tag{4}$$

where q_i represents the von Kries corrected quantum catch for each eggshell spectrum and q_j represents the von Kries corrected quantum catch of the corresponding background substrate spectrum for each eggshell (Vorobyev *et al.*, 1998a). We calculated ΔS and ΔL using the mean eggshell background reflectance spectra for each species and the mean reflectance spectra for the most appropriate nest substrate material for each species.

To complement our estimates of eggshell conspicuousness using receptor noise-limited models, we used TETRACOLORSPACE with MATLAB 7 (Stoddard *et al.*, 2008) to analyse ratite and galliform egg colours in avian tetrahedral colour space (Goldsmith, 1990; Kelber *et al.*, 2003; Endler *et al.*, 2005a; Stoddard *et al.*, 2008, 2011b). For ratite egg colours, we used standard UVS cone-type sensitivity curves available from Endler and Mielke (2005a). For galliform egg colours, we used VS cone-type sensitivity curves for peafowl (Hart, 2002). In addition, we plotted nesting substrate spectra in colour space. Figure 2 shows the gamut, or full range, of ratite (A) and galliform (B) colours compared to the full range of possible nest substrates. If ratites have more conspicuously coloured eggs than galliformes, then we expect the distribution of ratite egg colours in colour space to be further apart – compared to the distribution of galliform eggs – from the distribution of ground/nest colours.
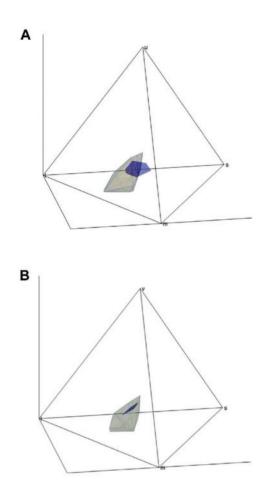
Figure 2 The distribution of eggshell background colour (blue convex hulls) and nesting substrate (brown convex hulls) plotted within an avian tetrahedral colour space for A) ratites with UVS vision, and B) galliformes with VS vision. For each of these plots, we used all nesting substrates used in this study. The ratites (*N* = 26) have a larger volume within this colour space than the galliformes (*N* = 15), indicating that to a conspecific these eggs exhibit a wider range in eggshell background colouration. It is important to note that, although this makes sense, the sampling effort was not equal between these two groups, which likely inflated the "gamut" of ratite egg colours relative to galliform egg colours. The tetrahedral analyses presented here are therefore qualitative rather than quantitative. The areas where the eggshell background colour do not overlap the nest substrate colour space distribution represent eggshells that would appear conspicuous against any of these backgrounds. A large volume of the ratite colour space does not overlap with the nest backgrounds, which is largely due to the bright blue-green eggshell ground colouration of *Tinamus* spp.

2.3 Phylogenetic reconstruction

We used Mesquite (version 2.6) to reconstruct a composite phylogeny representing the relationships between the species used in this study (Figure 3). We combined data from numerous published sources, including recent hypotheses for relationships among all birds (Ericson *et al.*, 2006; Hackett *et al.*, 2008), preferentially choosing molecular phylogenies. The relationships within the
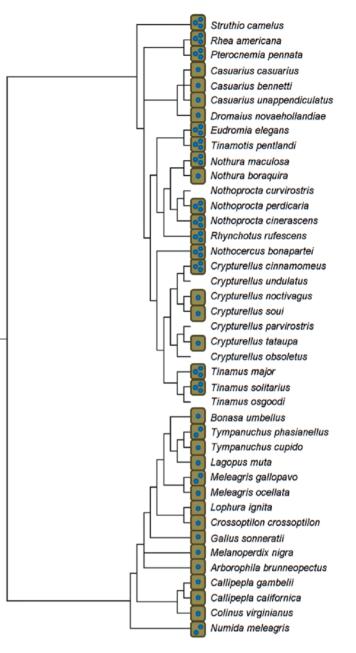

Figure 3 A composite phylogeny representing the relationships among and between the ratites and galliformes that formed the basis of our comparative tests. The nest symbols next to each name indicate solitary nesting (single circle), occasional egg dumping (two circles), and communal laying (three circles).

ratites rely heavily on a recent broad comparative analysis (Harshman *et al.*, 2008), while the finer relationships among the tinamous depend on a taxonomy (Bertelli *et al.*, 2004). The relationships among the galliformes follow Crowe *et al.* (2006).

2.4 Statistical analysis

All continuous variables that significantly deviated from normality (Shapiro-Wilks test) were Box-Cox transformed

prior to further analysis. We accounted for phylogenetic dependence with phylogenetic generalised least squares (PGLS) regressions using the package 'ape' in the statistical package R (R Development Core Team, 2010). For these analyses we used the maximum likelihood value of Pagel's λ (Pagel 1997, 1999), restricted between 0 and 1. This transforms a phylogeny to provide the best fit of the data to a Brownian motion model of evolution (Freckleton *et al.*, 2002). We ran two separate analyses to compare the conspicuousness of ratite and galliform eggs.

Since our reflectance measurements were taken on the eggshell background colour only, we did not have spectral data for eggshell speckles. Therefore, our estimates of discriminability provide information on how well background eggshell colouration matches the nesting substrate. For speckled eggs, this likely overestimates the degree of eggshell conspicuousness. To account for this, we ran two separate analyses to compare the conspicuousness of ratite and galliform eggs. Our first set of analyses used eggshell background colour data only, ignoring the influence of speckling. In our second set of analyses, we followed Kilner (2006) in classifying speckling as none (0), moderate (1), or heavy (2) to account for variation in eggshell speckling. Simply controlling for speckling as a covariate in our analysis would imply that we had a reason to expect that a heavily or moderately speckled egg would have a different background eggshell colouration than an unspeckled egg. We had no such expectation; therefore, we performed a transformation of our data such that the discriminability estimates were decreased by 20% for each level of speckling (*e.g.* an unspeckled egg was not reduced, while a heavily speckled egg was reduced by 40%, and a moderate speckled egg by 20%). This roughly accounts for the fact that the degree of egg speckling, produced by brown or olive-green protoporphyrin (Kilner 2006), influences the extent to which the eggshell background colour is visible. It does not account for the fact that egg speckling almost certainly affects overall egg conspicuousness in other ways (*e.g.* by providing disruptive camouflage), and future studies should address this explicitly (Stoddard *et al.*, 2011).

3. RESULTS

We found that when viewed by conspecifics the eggshells of galliformes and ratites (including tinamous) all showed chromatic contrast with nest materials (Figure 4; mean ± SD: 5.45 ± 3.24 just noticeable difference [JND]; range: 2.09 to 15.77 JND). The vast majority of species also exhibited substantial achromatic contrast with nest materials (mean ± SD: 32.45 ± 15.29 JND; range: 0.2253 to 54.12 JND). Contrary to our expectations, after controlling for the effect of shared ancestry, the background colour of the eggs of tinamous and other ratites were not significantly more conspicuous than those of galliformes, considering either chromatic variation ($F_{1,39}$ = 1.67,
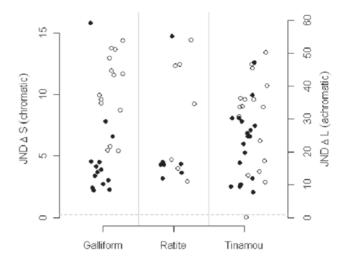

Figure 4. The calculated chromatic (filled circles, left axis) and achromatic (open circles, right axis) just noticeable differences (JND) of eggs as they would appear to a conspecfic against a natural background, plotted for galliformes, non-tinamou ratites, and tinamous. The vertical grey lines separate these avian groups, and the grey dashed line indicates a just noticeable difference of one, above which eggs would be noticeably different from their nest.

P = 0.20) or achromatic contrast ($F_{1,39}$ = 0.04, P = 0.84). However, after we applied a transformation to account for the reduced conspicuousness attributable to speckling, we found that ratite eggshells were more conspicuous than galliform eggshells when considering chromatic ($F_{1,39}$ = 5.47, P = 0.02) but not achromatic contrast ($F_{1,39}$ = 0.02, P = 0.90).

We found no support for the predictions of the communal laying hypothesis. Species that are known to lay communally do not have eggshells exhibiting greater chromatic conspicuousness ($F_{1,19}$ = 0.24, P = 0.63) or achromatic conspicuousness ($F_{1,19}$ = 0.05, P = 0.83).

4. DISCUSSION

To understand the functional significance of avian eggshell colour we must consider the visual abilities of relevant receivers, but most studies have focused on colour metrics independent of any particular visual system (Soler *et al.*, 2005, 2008; Avilés *et al.*, 2006, 2007; Morales *et al.*, 2006, 2008; Hanley *et al.*, 2008, 2009). We found that ratite egg colouration was no more conspicuous to conspecifics than galliform egg colouration was. However, when we accounted for speckling, we found that ratite eggs were more conspicuous than galliform eggs. This variation in eggshell conspicuousness was not explained by communal laying in ratites; therefore we were unable to support the hypothesis that eggshell conspicuousness may serve as signal of nest location for females.

We found that the average eggshell background colouration of both ratite and galliform eggshells differed from their nest substrates. This is no surprise in the

ratites, especially the tinamous (Lancaster, 1964; Weeks, 1973; Schwartz *et al.*, 1984; Brennan, 2009, 2010), but somewhat surprising for the galliformes, whose eggs generally appear cryptic (Baicich *et al.*, 1997). Contrary to our expectations, we did not find that the ratite eggshell background colour was more conspicuous than galliform eggshell background colour. At first, this finding appears counterintuitive because, at least to human eyes, ratite eggs appear to be strikingly more conspicuous. However, after correcting for the influence of eggshell speckling, we found that ratite eggs were significantly more conspicuous than galliform eggs. These findings suggest the importance of accounting for the whole nest, including the patterning and colouration of all eggs and the nesting substrate, when asking questions related to the conspicuousness of birds eggs. In future analyses, it would be preferable to collect reflectance spectra from the egg speckles themselves (Stoddard *et al.*, 2011c) and to assess speckling patterns quantitatively (Spottiswoode *et al.*, 2010; Stoddard *et al.*, 2010, 2012) Here, we used an approximation to reduce the overall conspicuousness of eggs that have speckles, but further research is necessary to understand how speckles interact with background eggshell colour and nesting substrate to reduce conspicuousness. Future work should consider more comprehensive approaches. One such approach would be to randomly collect numerous reflectance measures within and around each egg, which can then be used to quantify the conspicuousness of individual eggs or whole clutches.

Tinamous provide dramatic interspecific variation in eggshell colouration and colours unique among birds (Walters, 2006), but surprisingly little is known about the colouration of their eggs. We found that conspicuous eggshell colouration is not correlated with communal nesting, and therefore the hypothesis that egg colouration signals nest location to other females (Weeks, 1973; Brennan, 2010) was not supported. However, during the course of a field experiment, female great tinamous (*Tinamus major*) laid their eggs in artificial nests (Brennan, 2009, 2010), suggesting that eggs may sometimes serve as a visual signal or cue of nest location.

One factor that could have influenced our analysis is that the eggshell colour we measured in the museum collections may not accurately reflect the fresh colouration of eggs visible to females (or males) in nature. This is because the colouration of ratite eggs can change dramatically over time as a result of photo-oxidation (Figure 1, Brennan, personal observation), a phenomenon that is known to occur relatively rapidly in other avian groups (Cassey *et al.*, 2010a; Moreno *et al.*, 2011), and that perhaps explains why colour descriptions of tinamou eggs are so varied in the literature (Davies, 2002; Brennan, 2010). Fading should increase achromatic contrast and decrease chromatic contrast with the nesting substrate. Therefore, it is possible that our estimates of chromatic conspicuousness are lower and our estimates of achromatic contrast are higher than if we had measured

fresh eggshells. However, since all the eggs we measured were similarly old, our results should be comparable had we measured fresh eggs instead.

An alternative hypothesis that may explain egg colouration in ratites is that temporal changes in egg colour caused by fading could be used as a signal by females searching for nests in the early stages of laying in communal nesters Ratite chicks are precocial and therefore it is important that females add their eggs to the clutch early enough for those eggs to hatch. We suggest that eggshell pigmentation could provide information on the timing of egg laying in communal nesters, and further investigation of this hypothesis would be encouraged. Another potential limitation is that our conclusion is dependent on our current understanding of tinamou nesting and mating behaviour, and this group is poorly studied. We hope that our findings promote research on the behaviour of tinamous, as well as other tropical species for which little natural history information exists. Finally, one of the shortcomings of testing comparative hypotheses is that it is difficult to account for cases where traits are maintained because there is no selection against them. In our case, if the ancestors of ratites had conspicuous eggs and communal nesting, conspicuous eggs could be maintained even when species become solitary nesters if egg colour has little impact on predation pressure (Brennan, 2010).

It is interesting to note that without eggshell speckling, the galliform eggs were just as conspicuous to a conspecific as the ratite eggs. The role of predator pressure is often cited as an important role in the evolution of eggshell colouration and speckling (Wallace, 1889; Abercrombie, 1931; Stoddard *et al.*, 2011a). The ancestral eggshell colour is believed to be plain white (Wallace, 1889; Packard *et al.*, 1980; Kilner, 2006) because bird's closest living relatives have unpigmented eggshells (Packard *et al.*, 1980). Therefore the ancestors of modern birds most likely had eggshells that appeared quite conspicuous against ground or nest substrates, which could have generated strong selection for camouflaged appearance. However, a variety of evolutionary trajectories were available to their descendents. Some species may have sidestepped egg camouflage by evolving unique parental behaviours, while other species could effectively reduce these pressures by evolving eggshell speckling. A hierarchically nested simulation-based approach would be a fruitful future direction to examine if the current variation in eggshell background colours and speckling patterns can be explained by different evolutionary strategies (either increased egg speckling or increased parental care).

The visual models that we used for this research rely on our current understanding of the physiology of these birds rather than their behaviour. Behavioural experiments allow us to determine whether colour differences produce meaningful responses in organisms (Moreno *et al.*, 2006; Soler *et al.*, 2008), while the corresponding visual models will provide insight into whether those

transmitted signals contain the information we presume (Cassey, 2009). Therefore, field research should ideally combine behavioural experimentation and visual modelling. We encourage this holistic approach for future studies investigating the potential role of egg colouration as an intraspecific signal. In this study, we investigated egg conspicuousness from the perspective of other avian conspecifics. In the future, it would be productive to incorporate different models of predator perception (*e.g.*, avian, mammalian, reptilian) into studies of egg colouration to investigate possible trade-offs between egg conspicuousness and camouflage (Stoddard *et al.*, 2011a). To do this, it will be important to determine the extent to which predators rely on visual *versus* non-visual cues to locate nests.

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