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Do Ostriches *Struthio camelus* reject parasitic eggs by making use of colour as a cue?

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The Ostrich communal breeding system involves several females laying in a single nest. Only the 'major' female and the territorial male, however, provide parental care from incubation to fledging of chicks. Eggs are turned and displaced frequently upon the onset of incubation, and the major female evicts excess eggs out of the nest when the number of eggs is above a specific threshold level. A previous study indicated that the major female ostrich recognises her own eggs and selectively evicts eggs of minor females based on size, shape and shell texture. Our aim was to investigate if accepted and ejected eggs differ in colour characteristics. We quantified colour by measuring egg reflectance spectra, which were subsequently analysed using a visual model approach. Within clutches, there were no significant differences in colour between accepted and ejected eggs. These results suggest that female ostriches do not discriminate against foreign eggs based on deviations in colour.

Introduction

Ostriches *Struthio camelus* are primarily polygynandrous with both sexes mating with multiple partners (Sauer and Sauer 1966, Bertram 1992, Kimwele and Graves 2003). Several females may lay in a nest (communal nesting) whereby the first female to lay is considered as the 'major' female and those that subsequently lay in the same nest are referred to as 'minor' females (Sauer and Sauer 1966, Hurxthal 1979, Bertram 1992, Kimwele and Graves 2003). However, in such cooperative breeding, guarding and incubation of the nest is the responsibility of the major female during the day and the territorial male during the night (Bertram 1992, Kimwele and Graves 2003), though this rule is not invariable (Bertram 1992, FJM pers. obs.).

The major female lays on average 11 eggs (range 8–16) (Bertram 1992), while 1–7 minor females may lay 20–40 additional eggs in the nest, which is considerably in excess of the number that can be incubated (Sauer and Sauer 1966, Hurxthal 1979, Bertram 1992). The clutch before incubation may therefore contain as many as 30–40 eggs (Leuthold 1977, Bertram 1979). At the onset of incubation, eggs are turned and moved from one position to another to stimulate embryo growth (Hallam 1992, Deeming 1997), and it is at this stage that some of the eggs are ejected from the nest (Bertram 1992).

Lack (1947) documented that clutch size in some precocial species has an upper limit set by the incubation capacity of the parent ('the incubation capacity hypothesis'). Probably because an ostrich pair is able to successfully incubate only about 20–21 eggs (Hurxthal 1979, Bertram 1979, 1992), some excess eggs are rejected by the major female by pushing them up to 2 m away from the nest where they remain unincubated and will never hatch (Sauer and Sauer 1966, Bertram 1979, 1992). Bertram (1979, 1992) argued that major ostrich females benefit from extra eggs against predation through dilution effects, indicating that host females should accept parasitic eggs to some extent. Therefore, acceptance of some parasitic eggs can be advantageous as long as the number of eggs is below a certain threshold level (Bertram 1979, 1992).

Egg-laying by minor females can be regarded as a case of intraspecific brood parasitism, which has been reported to occur mainly among colonially breeding (Yom-Tov 2001) and precocial birds (Yom-Tov 1980, Bertram 1992, Yom-Tov 2001). Generally, brood parasitism is disadvantageous to the host female in terms of fitness costs (Bertram 1992, Lyon 2003). Studies on interspecific avian brood parasitism have supported egg discrimination by hosts as a coevolved anti-parasite strategy (e.g. Davies and Brooke 1989, Rothstein 1990, Moksnes et al. 1991). Lyon (2003) found that American Coots *Fulica americana* are able to recognise and reject eggs laid parasitically by conspecifics. In addition, experimental studies have shown that several passerines are able to recognise and reject a range of conspecific eggs (e.g. Welbergen et al. 2001, Procházka and Honza 2003, 2004, Avilés 2004, Honza et al. 2004, Stokke et al. 2004, Antonov et al. 2006a, 2006b, Vikan et al. 2009, 2010).

Visual cues are of critical importance to hosts in discriminating between their own and foreign eggs (e.g. Brooke and Davies 1988, Davies and Brooke 1988, Stokke et al. 1999, 2005, Polacikova et al. 2007, Antonov et al. 2008, Moskat et al. 2008, Lopez-de-Hierro and Moreno-Rueda 2010). Ostrich eggs are immaculate creamy white and it is difficult,

at least to the human eye, to differentiate between the eggs of the different females. Thus, the risk of committing errors in recognition and rejection of foreign eggs (e.g. Lotem et al. 1995, Davies et al. 1996, Stokke et al. 2005, 2007, Moskát and Hauber 2007) may be high in this species, potentially rendering recognition based on colour are error prone and difficult task for major ostrich females. Moreover, Bertram (1979, 1992) indicated that major ostrich females recognise minor female eggs by using eggs size, shape and surface texture relative to their own eggs as cues rather than colour. However, colour differences among the eggs of major and minor females were not quantified in an objective way in the latter studies, making it difficult to conclude if colour plays a role in rejection decisions by major females.

Previous studies have shown that avian colour vision differs from that of humans. For instance, many bird species are sensitive to the ultraviolet (UV) part of the spectrum (Bennett and Cuthill 1994, Cherry and Bennett 2001), and furthermore, they also typically possess four cone types which provide the opportunity for tetrachromatic vision (Chen and Goldsmith 1986). Previous studies have shown that ostriches do indeed possess four cone types, but that the peak sensitivity at the shortest wavelengths is just above the UV part of the spectrum (405 nm, i.e. the 'violet' part of the spectrum) in contrast to many passerine species in which the peak sensitivity of this particular cone is actually within the UV region (Wright and Bowmaker 2001, Hart and Hunt 2007). Furthermore, it has been suggested that ostrich females may adjust their investment in eggs according to perception of male quality based on the 'violet' part of the colour spectrum (Bonato et al. 2009). These studies therefore highlight the importance of an objective quantification of egg colour reflectance together with a consideration of which cognitive stimuli the target bird species actually can perceive.

Our aim was to investigate if accepted eggs differed in colour characteristics from rejected ones. In order to investigate if this was the case we compared colour contrasts between accepted and rejected ostrich eggs within single clutches by using the tetrahedral colour space visual model (Stoddard and Prum 2008). If ostriches use colour as a cue in foreign egg discrimination, we predicted greater within-clutch differences in colour contrasts between accepted and rejected eggs than between accepted eggs.

Methods

The study was carried out in the Serengeti National Park (SNP) in Tanzania (14 763 km^2) between October and December 2006. During the study, most ostrich nests were found in plain grasslands, their preferred habitat (Bertram 1992). To minimise disturbance, nests were visited once or twice a week during the egg-laying and incubation period. A total of 24 nests were found, but most of the nests were predated in the egg-laying stage.

We measured spectrophotometric reflectance of two accepted eggs from each clutch and one or two rejected eggs (if more than one egg was rejected) from all nests with rejected eggs (N = 6). Consequently, analyses were based on 12 accepted and 10 rejected eggs.

Reflectance spectra in the range 300–700 nm were obtained from the 22 eggs using a spectroradiometer (Ocean Optics, Duiven). Colour was measured once on three randomly selected approximately 1 mm^2 areas of the surface of the eggs, in the pointed and blunt ends and in the middle of the egg. The light was transferred to the eggs through a quartz optic fiber (Ocean Optics) probe that reached the eggs at an angle of 45° from the light source and transferred reflected light to the spectrometer. A reference and dark calibration were made prior to the measurement of each clutch. Data from the spectrometer were passed into a computer through OOIBase 32 software (Ocean Optics)

Since ostriches lay immaculate eggs, we calculated the mean reflectance spectrum for each egg based on the three spectra obtained as explained above. To quantitatively describe egg colour, we analysed the spectra within the framework of Goldsmith's tetrahedral colour space model (Goldsmith 1990), which has recently been strongly recommended for analysing colour patterns in tetrachromates, such as birds (Stoddard and Prum 2008). This model uses idealised stimulus values (Q_i) calculated for each of the four avian cone types according to the formula:

$$Q_i = \sum_{\lambda=300}^{700} R(\lambda) S_i(\lambda)$$

where $R(\lambda)$ is the reflectance spectrum of an egg, and $S_i(\lambda)$ is the spectral sensitivity for cone i. Since ostriches are violet-sentitive (Wright and Bowmaker 2001, Hart and Hunt 2007, Bonato et al. 2009), we used the average spectral sensitivity curves for V-type retinas as given by Endler and Mielke (2005). The values for S_i, R and the resulting Q_i were normalised to sum to 1. Goldsmith's (1990) formula treats the irradiance spectrum as a constant at all wavelengths with an integral of 1 (Stoddard and Prum 2008).

The four Q_i values form a (v, s, m, l) vector of the relative stimulation of violet-sensitive, short wavelength-sensitive (blue), medium wavelength-sensitive (green) and long wavelength-sensitive (red) cone photoreceptors. Thus, a colour can be represented as a point in a tetrahedron whose vertices coincide with v, s, m, and l cone stimulation equalling 1.The achromatic point corresponds to equal (0.25) stimulation of all the four cone types. For more details on the application of the model see Stoddard and Prum (2008).

The overall colour contrast between any two eggs was expressed as the Euclidian distance of their respective coordinates (X, Y, Z) in the tetrahedron (Endler and Mielke 2005). Colour contrasts calculated this way are highly correlated to discriminability values resulting from Vorobyev and Osorio's (1998) noise-limited colour opponency model but without specifying a threshold discrimination value (Vikan et al. 2009). In addition, we also calculated hue disparity between eggs following Stoddard and Prum (2008).

To determine whether ostriches use deviations in colour to discriminate against foreign eggs, we compared the colour contrasts between two randomly selected accepted eggs with the mean colour contrast of each of these eggs with the two eggs that were rejected from the same nest. We predicted that accepted eggs should show a lower contrast with respect to each other than their mean contrast

with the rejected eggs, and we tested this via paired *t*-tests for both colour contrast and hue disparity. All calculations and statistical analyses were performed in R.2.10.0 (http://www.R-project.org).

Results

Within ostrich clutches, the deviation in colour between rejected and accepted eggs was not significantly different from the deviation between accepted eggs (Figure 1). This was evident in both colour contrast ($t_5 = 0.82$, $P = 0.45$) and hue disparity ($t_5 = -0.16$, $P = 0.88$).

Discussion

To the best of our knowledge, this is the first study to test objectively if ostrich females use differences in colour in their rejection decisions. Since rejected eggs were not detectably more contrasting in colour from accepted eggs than were the latter with respect to each other, major ostrich females do not seem to discriminate against minor female eggs based on differences in egg colour. A possible reason for this may be that variation in colour of ostrich eggs is generally low and that variation within females is not markedly lower than variation between females. Therefore, a probable scenario is that conspecific parasitic eggs cannot be discriminated by colour because they fall below the cognitive threshold for recognition (see Rodríguez-Gironés and Lotem 1999, Stokke et al. 2005, Hauber et al. 2006, Stokke et al. 2007). Recognition based on colour would therefore be error-prone and unreliable.

Our results seem to be in accordance with other studies on birds laying more or less immaculate eggs and which have difficulties recognising foreign eggs by using colour cues (Moksnes and Elvertrø 2006, Siefferman et al. 2006, Underwood and Sealy 2006). Species with maculated eggs, however, are often able to recognise and reject a considerable proportion of conspecific eggs as long as they are contrasting somewhat in appearance from own eggs (e.g. Welbergen et al. 2001, Procházka and Honza 2003, 2004, Avilés 2004, Honza et al. 2004, Stokke et al. 2004, Antonov et al. 2006a, 2006b, but see Antonov et al. 2006c).

Nonetheless, major ostrich females are able to reject foreign conspecific eggs (Bertram 1979, 1992). A recent molecular study (Kimwele and Graves 2003) provided additional support for this because major females incubated more of their own eggs than would be expected if they were incubating all eggs at random. Objective quantification of colour differences in our study suggests that ostriches do not apparently use deviations in colour to discriminate against foreign conspecific eggs. Rather, they may rely on other potential cues such as differences in size, shape and surface texture (Bertram 1979, 1992), but the relative importance of these egg traits is unclear and needs further investigation.

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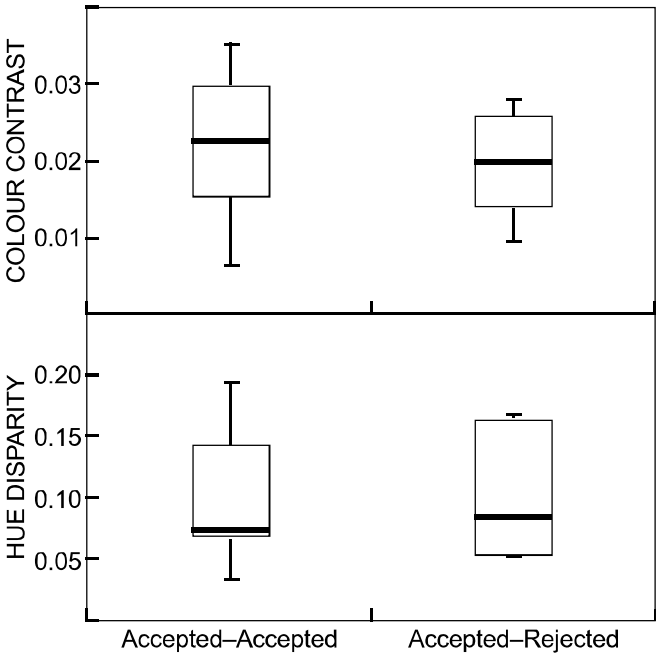


Figure 1: Differences between accepted and rejected eggs within six ostrich clutches in colour contrasts (A) and hue disparity (B) as calculated from tetrahedral colour space visual model (Stoddard and Prum 2008). Two accepted and two (one) rejected eggs were measured per clutch

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