Is egg colouration and clutch mass indicative of female condition in European starlings (*Sturnus vulgaris*)?

By

Matthew Porter

A Thesis Submitted to

Saint Mary's University, Halifax, Nova Scotia

In Partial Fulfillment of the Requirements for

the Degree of Bachelor of Science (Honours) in Biology.

April, 2014, Halifax, Nova Scotia, Canada

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Approved: Dr. Colleen Barber

Supervisor

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Approved: Dr. Susan Meek

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Abstract

Avian egg mass and colouration have been correlated with female condition, in that eggs of greater mass and colouration intensity have been shown to have a positive relationship with female condition. Individuals that display high-quality traits at a greater intensity than others are preferred as mates, as intensity is positively correlated to condition. Assessment of ornaments is done by both sexes. In this study, I correlate female condition of European starlings (*Sturnus vulgaris*) with egg mass and colourmetric values. I predicted females in better condition would have eggs of greater mass and more intense blue-green chroma. I estimated condition from morphometric measurements collected from 28 females. Condition was correlated with mean egg mass/clutch mass, total egg mass/clutch mass, egg shell colour component values (hue, UV reflectance, and chroma) to determine if these egg characteristics were honest indicators of female condition. Female condition was not correlated with egg mass or egg colouration. These results do not support my prediction that females in better condition would lay heavier eggs and/or eggs with greater blue-green colour intensity. These results suggest that egg characteristics are not as an indication of female quality.

Date: April 28, 2014

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Introduction

Intersexual selection is the process by which members of a species are able to assess the genetic quality of a potential mate through secondary sexual characteristics, whether they are aesthetic or functional traits, and determine if that individual is of high or low quality (Burley, 1986; Holland, 2002; Holland and Rice, 1998; Murphy, 1998; Warner and Schultz, 1992). The traits are generally costly to display, heritable to offspring and are not always directly linked to reproduction or survival of that individual (Safran et al., 2013). An individual that displays high-quality traits becomes very attractive to prospective mates as it shows that the individual can endure the costs associated with displaying such traits; individuals that display high-quality traits at a greater intensity than others are preferred as mates (Burley, 1986). Burley (1986) proposed two hypotheses in relation to the degree of attractiveness of individuals of both sexes and the level of parental investment they would obtain from a mate. The differential–access hypothesis states that in species where both parents are involved in parental investment of the offspring, an individual's level of attractiveness, regardless of sex, is related to its ability to attract mates, resulting in more attractive individuals being able to be more selective in choosing mates (Burley, 1986). The differential–allocation hypothesis states that an individual's level of attractiveness will determine the amount of parental investment from their mate, resulting in more attractive individuals securing a higher degree of parental investment from their mate. The advantage to the mate is that he/she continues to have reproductive access to the attractive individual; the benefit to the

attractive individual is that they can reduce their parental investment, which can result in a longer lifespan and greater reproductive success (Burley, 1986).

Eggs, in particular, egg mass and egg colouration, have been shown to signal female condition in tree swallows (*Tachycineta bicolor*) (Ardia et al., 2006), herring gulls (*Larus argentatus*) (Bogdanova et al., 2006), spotless starlings (*Sturnus unicolor*) (Lopez-Rull et al., 2008), European starlings (*Sturnus vulgaris*) (Meijer and Langer, 1995), pied flycatchers (*Ficedula hypoleuca*) (Morales et al., 2008; Moreno et al., 2004), Eastern bluebirds (*Sialia sialis*) (Siefferman et al., 2006), and great tits (*Parus major*) (Visser and Lessells, 2001)

Egg mass is a characteristic that has received considerable attention in relation to female quality. Studies have shown that there is a strong positive correlation between egg size and nestling growth and survival (e.g. Smith et al., 1993; Szigeti et al., 2007). All the resources and nutrients the growing embryo require to develop fully are contained within the egg; larger eggs result in larger, healthier offspring as is documented in herring gulls (Bogdanova et al., 2006), thick-billed murres (*Uria lomvia*) (Birkhead and Nettleship, 1982) , and razorbills (*Alca torda*) (Hipfner, 2000). Research has indicated that egg mass directly relates to female quality due to the significant amount of energy that is required to produce eggs and supply embryos with the nutritional requirements and antioxidant properties that enhance offspring survival rate (Szigeti et al., 2007). The procurement of the resources the female requires for egg formation is costly (Visser & Lessells, 2001), and may be the most important factor for egg formation (Ardia et al., 2006). Smith et al.'s (1993) study on European starlings indicated a strong positive relationship between

female quality and female condition. High-quality females are better able to obtain

greater food resources by pairing with a high-quality male who defends a highly

resourceful territory (Yasukawa, 1981), and also by utilizing their own foraging abilities

(Ardia et al., 2006; Meijer and Langer, 1995; Rutkowska and Cichon, 2002). Again,

Burley's (1986) differential–allocation hypothesis is demonstrated in the relationship

between egg mass and female quality; higher quality females would produce larger eggs,

which would result in a higher provisioning rate by their mate during egg laying and

incubation, in comparison to lower quality females that would lay smaller eggs, resulting

in a lower provisioning rate by the male (Bogdanova et al., 2006; Smith et al., 1993).

There have been many hypotheses proposed to explain egg colour such as

protection against brood parasitism (Grim, 2005; Soler et al, 2000) and solar radiation by

reflecting its transmission to the embryo (Lahti, 2008; Westmoreland et al., 2007),

camouflage from predators (Weidinger, 2001), and strengthening the egg shell (English

and Montgomerie, 2011; Gosler et al, 2005). Moreno and Osorno (2003) proposed the

sexually selected egg colour hypothesis which suggests that females signal their quality to

their mates by the amount of pigment they use in egg colouration, as the intensity of the

colouration (more pigment) will indicate a higher fitness quality of the female. Most

studies related to egg colour have examined blue-green colouration (e.g. Lopez-Rull et

al., 2008; Morales et al., 2008; Moreno and Osorno, 2003; Moreno et al., 2004;

Siefferman et al., 2006; Soler et al., 2005). Blue-green egg colour is produced by the

pigment biliverdin which is produced by the breakdown of haem by the liver and then

deposited into egg shells by the shell gland (Moreno & Osorno, 2003, Siefferman et al,

2006). Biliverdin has antioxidant properties and aids in the removal of free radicals from the body; the buildup of the pigment in the shell gland releases steroids which result in oxidative stress (Krist & Grim, 2007; Moreno & Osorno, 2003; Moreno et al., 2004). The deposition of biliverdin into egg shells by females signals their ability to handle the accumulation of free radicals in their body during egg laying (a stressful time, and therefore costly) to their mate and provides them with a good indication of their mate's current physiological and immunocompetence levels (Krist & Grim, 2007; Moreno & Osorno, 2003; Moreno et al., 2004). Another benefit of biliverdin egg shell deposition is increased antioxidant abilities for offspring because the ability to produce biliverdin should be heritable and will result in future reproductive success (Lopez-Rull et al., 2008; Moreno et al., 2004; Soler at al., 2005). In accordance with Burley's (1986) differential-allocation hypothesis, the higher the quality of a female, the better she will be at depositing biliverdin during egg production, thereby increasing blue-green eggshell colouration. If the female has the ability to sustain the costs of producing the pigment, as pigment production is costly to produce in terms of losing antioxidant resources and coping with free radical accumulation in the female's body (Moreno and Osorno, 2003), this should result in more parental investment by the male because males acquire fitness gains by having better quality offspring (English and Montgomerie, 2011).

Blue-green colouration has been found to increase in intensity with an increase in female condition in Eastern bluebirds (Siefferman et al., 2006), and spotless starlings (Lopez-Rull et al., 2008). Also, high-quality females (defined by condition, age and body mass) lay heavier eggs as seen in the pied flycatcher (Moreno et al., 2004), the shag

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(*Phalacrocorax aristotelis*) (Amundsen and Stokland, 1990) and the European starling (Smith et al., 1993).

Avian visual systems have four classes of cone photoreceptors: long wavelength (red, approx. 560-700nm), medium wavelength (green, approx. 500-620nm), short wavelength (blue, approx. 400-540nm), and very short wavelength (ultraviolet/violet, approx. 300-420nm) (Endler and Mielke, 2005). The relative stimulation of the four cone classes can be converted to coordinates that are mapped within a tetrahedral colour space model (Figure 1) (Stoddard and Prum, 2008). The center of the tetrahedron, the achromatic origin, is the point where all four classes of cones are stimulated equally and this point represents the absence of color. Each vertex of the tetrahedron represents complete stimulation of only one cone class. The edges of the tetrahedron represent the relative stimulation of two classes of cones. The faces of the tetrahedron represent the relative stimulation of three classes of cones. A color that stimulates all four classes of cones is represented by a point within the tetrahedron (Endler and Mielke, 2005).

Hue and chroma describe a specific color and the intensity of that colour, respectively. Hue is defined by the direction of a color from the achromatic point (Figure 1). This vector is determined by the angles phi and theta. Phi is the angle of vertical displacement from the achromatic origin. Theta is the angle of horizontal displacement from the positive X-axis. Phi and theta are analogous to latitude and longitude on the earth, with phi being latitude and theta being longitude. The ultraviolet (UV) component of a hue is plotted along the Z-axis of the tetrahedron and the angle phi represents the relative stimulation of UV cones. The higher a data point is within the tetrahedron, the

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higher the UV reflectance component is for the hue. All possible intensities of a given hue fall on a straight line that runs from the origin to the surface of the tetrahedron. Chroma, denoted by r, is defined by the distance of a color point (phi, theta) from the achromatic origin; the greater the distance the colour point is from the achromatic point, the greater the colour color intensity. Maximum r values occur for pure hues, which lie at the vertices of the tetrahedron. Since the colour space is not a sphere, all other points in the tetrahedron have lower maximum chroma values. Hence, chroma is presented as r.achieved, which is the ratio of r to the maximum possible value of r for that hue (r/r_{max}).

European starlings form socially-bonded pairs, such that they are socially monogamous with their primary mate; their offspring receive biparental care (Wright and Cuthill, 1992). Males and females however can be facultatively polygamous, engaging in extra-pair copulations that may result in offspring produced outside of the socially-bonded pair (Gwinner and Schwabl, 2005; Pinxten and Eens, 1997; Wright & Cuthill, 1992). Male European starlings use sexual signaling to express their quality, and thereby their condition, to potential mates through song (Mountjoy & Lemon, 1996), amount of feather iridescence and body size (Wright & Cuthill, 1992). These traits are displayed to attract high quality females. European starlings are cavity nesters that lay three to six eggs, which are blue-green in colour (Cornell Lab of Ornithology, 2014). Eggs are laid at a rate of one egg per day and clutches are double-brooded (Feare, 1984). When egg laying is complete, incubation lasts for 10-12 days beginning when the last egg is laid and after hatching, nestlings remain in the nest and receive parental care for 21-24 days (Cornell Lab of Ornithology, 2014).

While the majority of studies on UV reflectance and the avian colour spectrum has focused on plumage as a medium for sexual signals and mate quality assessment, little investigation has been done on the role of UV reflectance of egg shells. If UV intensity in eggs is an indication of female quality, it is logical to predict a positive relationship between female condition and UV reflectance intensity of eggs.

The objective of my study is to examine whether there is correlational evidence that egg characteristics are indicative of female condition in European starlings. I predict females in better condition will have heavier eggs and that their eggs will have a greater intensity of blue-green colouration.
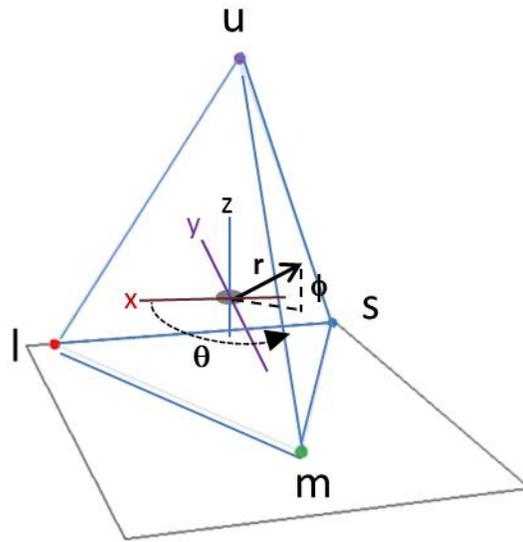
Figure 1. Tetrahedral colour space model. Vertices are labeled with cone type: ultraviolet

(u), short (s), medium (m), and long wavelength (l). The X and Y axes form a horizontal

plane within the color space and the gray dot is the achromatic origin. The bold arrow

represents a color vector. Angle θ (theta) shows the horizontal displacement of the colour

vector from the positive X-axis. Angle ϕ (phi) shows the vertical displacement of the

colour vector from the X-Y plane. Together, the coordinates (θ, ϕ) define hue. Colour

intensity (chroma) represented by the distance (r) of the colour vector from the

achromatic origin. (Image modified from Stoddard and Prum, 2008)

Methods

Study site and species

      Data were collected on Saint Mary's University campus in Halifax, Nova Scotia, Canada (44° 37' 54.07" N, 63° 34' 47.09"), from late April to late July 2013. On campus, there is a population of European starlings that nest in 45 artificial nesting cavities (nest boxes); boxes are attached to trees throughout the campus. The nest boxes are easily accessible with a ladder. Two broods were followed, denoted as early (n=14) and late (n=14) broods with a total of 226 eggs used in analysis.

Field methods

      The close proximity of nest boxes to the lab on campus made the collection of egg mass and spectroscopy data on egg shell reflectance feasible, with little disruption to parental care. Every nestbox was monitored daily prior to laying, beginning in late April. When an egg was laid, it was carefully removed and weighed with an AWS-250 electronic scale to the nearest 0.1g. The egg was then numbered on the blunt end with a black felt Sharpie-waterproof marker according to its place in the laying order for that clutch. For example, the first egg in a nest would be labeled 1, during nestcheck the next day the second egg would be labeled 2. After the weight for the egg was recorded, the egg was returned to the nest.

      Three days after laying was complete, each egg was analyzed for colour reflectance intensity. Clutches were removed from the nest and taken to a spectrometer inside our laboratory office. Only half of the eggs per clutch were removed at one time,

necessitating two trips for spectrometry measurements per clutch; complete clutches were

never removed at one time. A person was always present on a ladder under the nestbox

containing the eggs being measured to prevent adults from entering the nestbox while the

eggs were removed for measuring; this was done to prevent adults form abandoning the

nest. Eggs were absent from the nest for approximately 15 minutes.   An Avantes DH-

2000 UV-VIS-NIR Lightsource spectrometer containing a deuterium and a halogen lamp

was used to obtain these values. Connected to the spectrometer was a fibre-optic cable

that had a 2 mm light probe at the end. The blunt end of the egg was placed on the light

probe at approximately 45°, and three separate readings were taken. Placing the egg at a

45° prevented interference from the ink used in numbering the egg. The egg was carefully

rotated after each reading was taken so as not to measure the same spot twice. Ocean

Optics Inc. OOIBase32 v1.0.3.0 software recorded the readings and produced a graph for

each of the three measurements (Figure 2). The graphs displayed reflectance intensity (%)

on the Y-axis and wavelength (nm) on the X-axis, ranging from 300 to 700 nm.
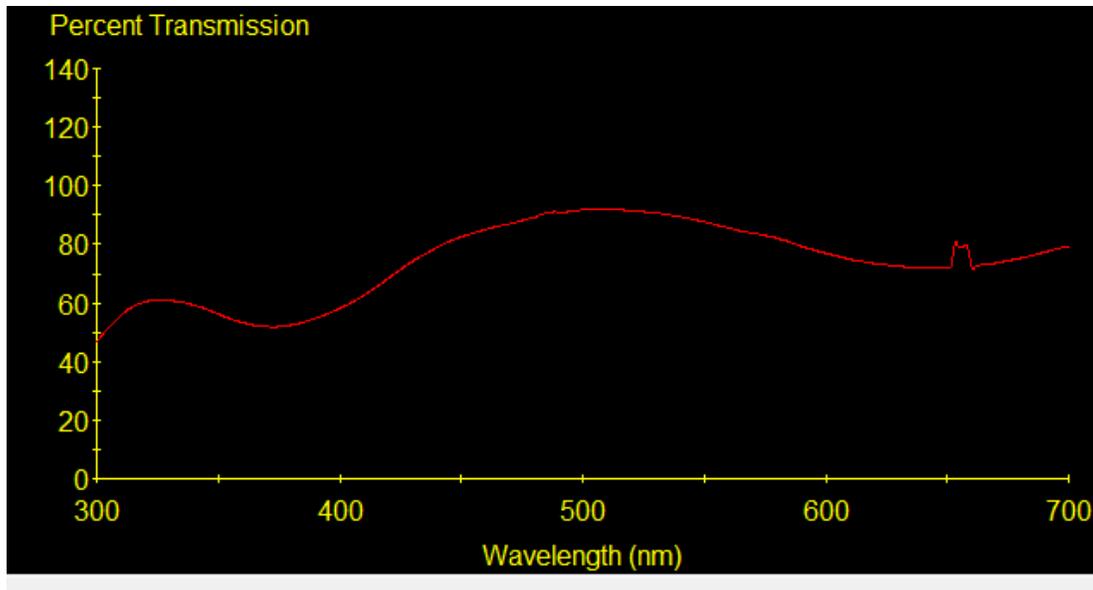
Figure 2. Example of reflectance spectra of a European starling egg shell. The line shows the percent reflectance for wavelengths across the avian visual spectrum, which ranges from 300nm to 700nm.

To obtain female morphometric data, females were caught in nestboxes using a nestbox trap, when nestlings were between five and thirteen days old (hatch day = day 0). Traps consisted of a piece of wood approximately 5x5" and 1" thick, attached to a hinge. The hinge was placed on the inside of the front wall of the nestbox and the wooden trap door was propped up with a twig inside the nestbox. When an adult entered the nestbox, they tripped the twig, resulting in the trap door blocking the nestbox entry hole, leaving the adult trapped. The adult was carefully removed and morphological data were taken. An adult's weight was measured by placing the adult in a nylon stocking attached to a Pesola spring scale and recording the weight to the nearest 0.5g. With digital calipers, the tarsus length of each adult was measured three times, to the nearest 0.01 mm, and the

average was calculated. Adult trapping was often attempted during early morning when

there was a high provisioning rate.

Data analysis

A least squares regression of female mass against tarsus was run and the residuals

were used to represent the index of female condition, with positive values relating to

better condition. Total egg mass was calculated for each clutch, as was mean egg mass.

Each of the three graphs produced by the spectrometer for every egg was analyzed by

CLR (Colour Analysis Programs v1.05) (Montgomerie, 2008). This software converts the

spectrometer-produced data into Excel files that contain both a graph and the numerical

values for the % reflectance at every nm wavelength between 300 and 700 nm. Spikes in

the graphs, due to background electronic noise, were removed using the CLR spike

removal feature, resulting in a smooth graph that displayed peaks of reflectance of the egg

shell. The three separate readings for each egg were averaged at every nm and copied into

a master spread sheet. This master spread sheet was then entered into Pavo (Perceptual

analysis, visualization and organization of spectral data v 0.0-1) (Maia et al., 2013)

through R v 3.0.2 (Becker et al., 2013).

R is a working platform that is used for producing, interpreting and analyzing

statistical data written in computer language. Pavo is a package for R that is used to

organize, process and visualize spectral data, and allows the user to analyze spectral data

based on receiver-specific visual models (Maia et al., 2013). These visual models use the

receiver's physiological visual system phenotype to interpret the data, measure cone

stimulation, and place cone stimulation within a tetrahedral colour space (Maia et al., 2013). Once the data are plotted within the tetrahedral colour space, colourmetric values, such as hue and chroma, can be calculated and observed (Figure 5) (Maia et al., 2013). For colour analysis, I examined three aspects of egg shell colour: hue, which is denoted by h.theta and represents the direction of a colour vector in the tetrahedral colour space (blue, green, red, ultraviolet); UV, which is denoted by h.phi and represents the amount of UV reflectance of the egg shell; and chroma, which is denoted by r.achieved and represents the intensity of the hue. Testing for normality of colour component spectra values was done using D'Agostino-Pearson omnibus normality test. Results were considered significant when $P \leq 0.05$.

Egg mass

Female condition residuals were not correlated with mean egg mass (r=0.270, n=28, P=0.17; Figure 3) and total egg mass/clutch (r=0.055, n=28, P=0.78; Figure 4).
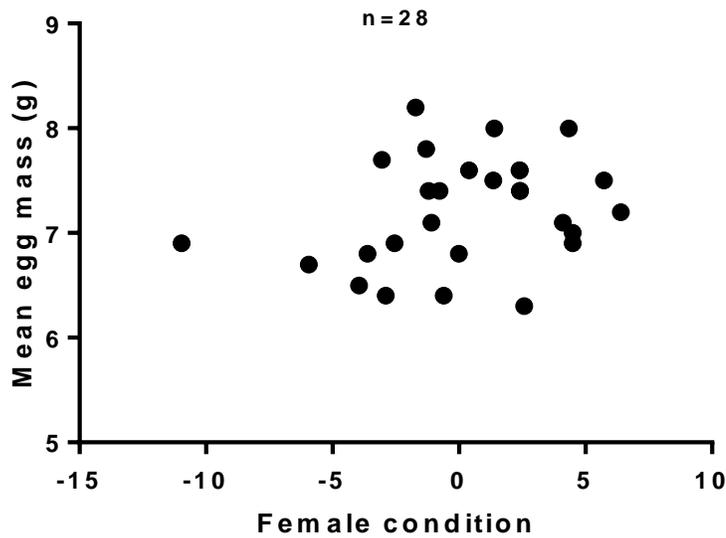

Figure 3. Relationship between mean egg mass (g) and female condition. Females with higher condition scores did not produce eggs of greater mean mass than females with lower condition scores.
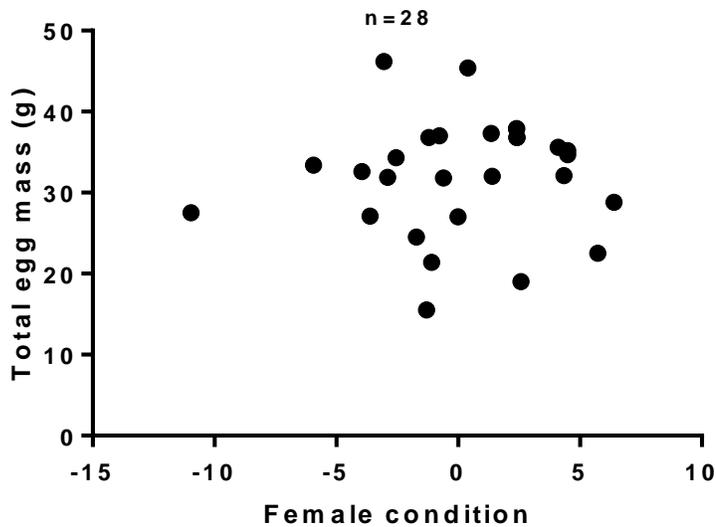
Figure 4. Relationship between total egg mass (g) and female condition. Females with higher condition scores did not produce clutches with higher total egg masses than females with lower condition scores.

Egg shell colour

Tetrahedral colour space was based on the European starling visual model and was calibrated with reflectance spectra from inside a nest box. Tetrahedral colour space plots of egg reflectance spectra show little variation in egg colouration. Hue vectors are tightly clumped below the X-Y plane and toward the u-m-l (ultraviolet-medium-long wavelength) side of the tetrahedron (Figure 5A). The data points are close to the achromatic origin, which indicates that the chroma of egg hues is low (Figure 5B). Based on the position of the data points in the tetrahedron, light reflected by egg shells

stimulated medium and long wavelength cones the most, with little stimulation of short and ultraviolet wavelength cones. According to this model, egg hues appear yellowish to European starlings. A Robinson projection is a two-dimensional representation of a sphere. Plotting the hue vectors, (θ, ϕ), from the tetrahedron onto the Robinson projection displays the variability in hue, independently of chroma. A Robinson projection of egg shell reflectance reveals that the variation in egg shell hue is spread from top to bottom, which is along the UV component of colour (Figure 6). Thus, egg shell hues vary in the amount of UV reflectance.
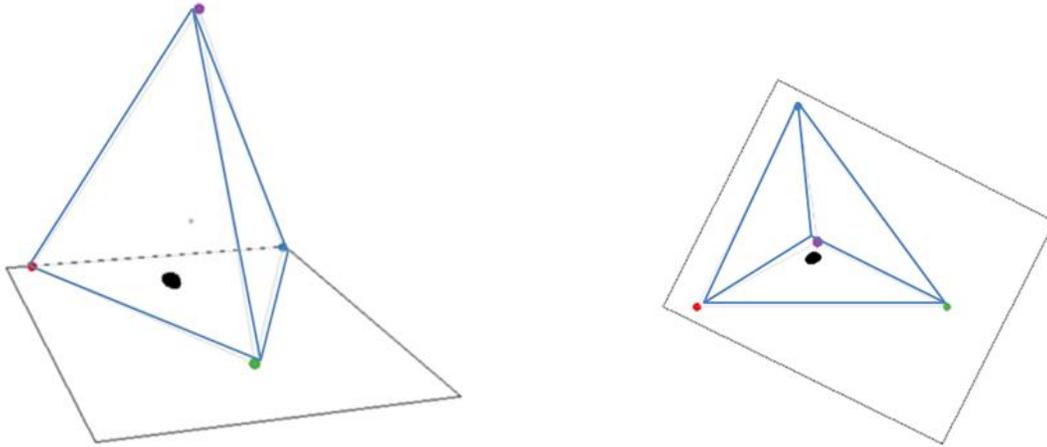
A   B

Figure 5. Tetrahedral colour space plots of egg shell reflectance according to the
European starling visual model. (A) Data points of the 226 eggs (black dot) are tightly
clumped between the medium and short wavelength vertisces and below the X-Y plane.
(B) View of the colour space from above. The achromatic origin (grey dot) lies beneath
the ultraviolet vertex. The data points are located close to the center of the color space,
indicating that the chroma of egg hues are low. (Image generated by Pavo analysis)
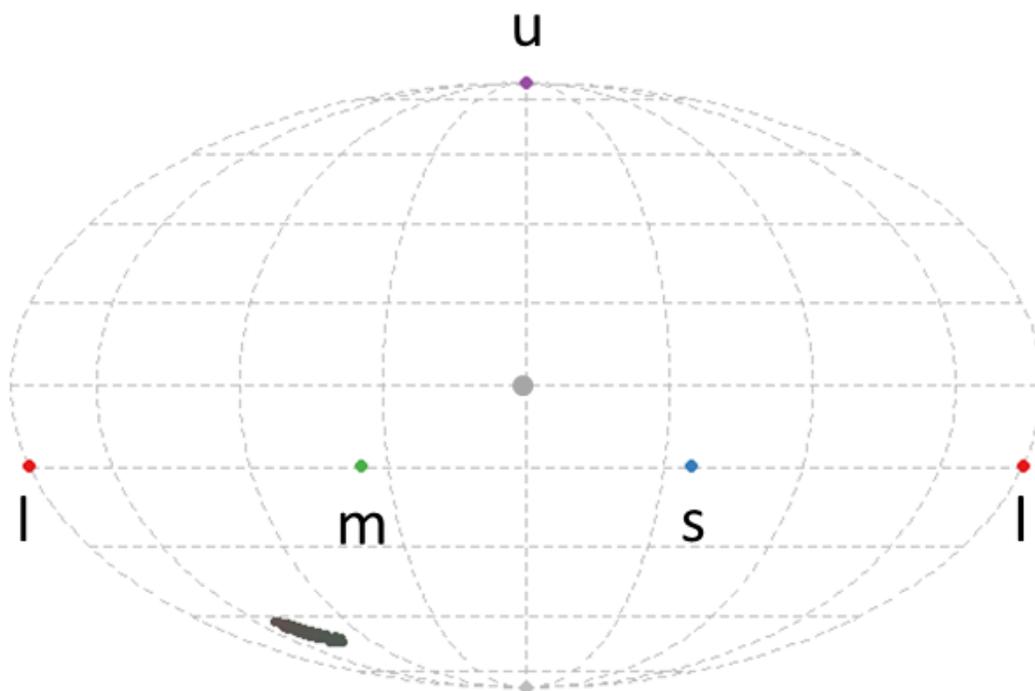
Figure 6. Robinson projection of egg hues according to the European starling visual model. The Robinson projection is a two-dimensional representation of a sphere. Colored dots represent the u (ultraviolet/violet wavelength), s (short wavelength), m (medium wavelength), and l (long wavelength) vertices of the tetrahedron. The gray dot is the achromatic origin. Hue disparity among the 226 eggs is viewed by plotting the hue vectors, (θ, ϕ), onto the Robinson projection. The distribution of dots (lower left) shows that the hue disparity lies along the UV component of colour. Egg shells that stimulate more UV cones also stimulate slightly more long wavelength cones. (Image generated by Pavo analysis)

Female condition residuals were not correlated with egg shell hue (r=0.123, n=28, P=0.53; Figure 7), egg shell UV reflectance (r=0.024, n=28, P=0.90; Figure 8), or egg shell chroma (r=0.104, n=28, P=0.60; Figure 9).
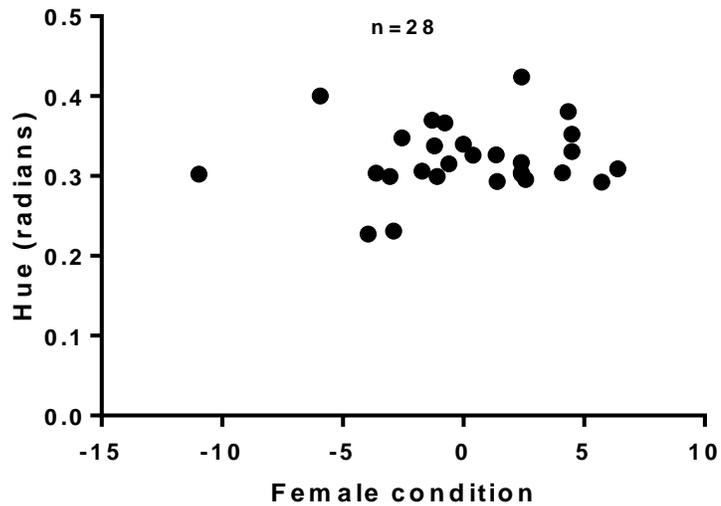
Figure 7. Relationship between female condition and egg shell hue. Egg shell hue did not vary with female condition.
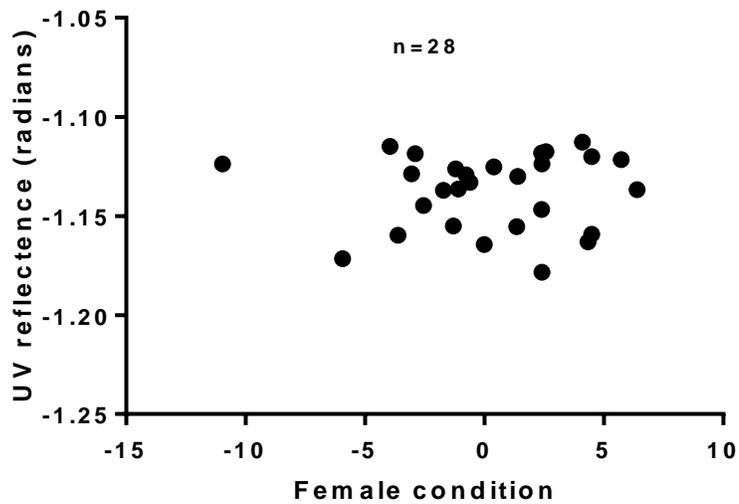
Figure 8. Relationship between female condition and egg shell UV reflectance. Egg shell UV reflectance did not vary with female condition.
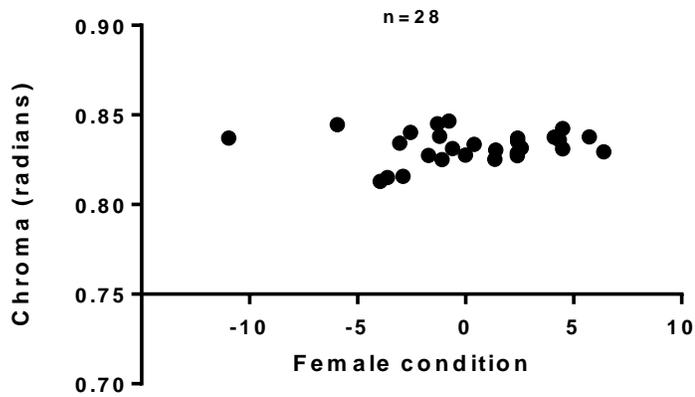

Figure 9. Relationship between female condition and egg shell chroma. Females with higher condition scores did not produce eggs that were more intense in colour than females with lower condition scores.

Discussion

Condition and egg mass

The prediction that females in better condition would lay heavier eggs than females in poorer condition was not supported in this study. A common assumption regarding egg mass, with observational and experimental support (e.g. Ardia et al., 2006; Styrsky et al., 1999), is that the greater the mean egg mass, the better the hatchling's survival to fledging due to an increase of nutrients and antioxidants present in the egg (D'Alba et al., 2007). These nutrients and antioxidants also contribute to the nestling's weight, size, growth, and immune capabilities (D'Alba et al., 2007; Wendeln, 1997; Whittingham et al., 2007). Styrsky et al.'s (1999) study on house wrens (*Troglodytes aedon*) documented a positive relationship between egg mass and female characteristics such as condition, age, and provisioning abilities. Resource allocation by females to egg production is costly and can affect a female's reproductive abilities and performance later in the breeding season (Ardia et al., 2006; Whittingham et al., 2007). Therefore, the better a female's condition, the more energy and resources she can allocate to egg production (D'Alba et al., 2007; Whittingham et al., 2007). The findings of previous studies relating female quality and egg mass have received mixed support (e.g. Saino et al., 2004; Smith et al., 1993; Wendeln, 1997; Whittingham et al., 2007)

Smith et al. (1993) examined if there was a relationship between egg mass and female quality in European starlings, as well as a relationship between egg size and nestling growth and survival. In this study, Smith et al. define high-quality females as

being good foragers, a skill permitted by being in good condition. Females were caught upon nestbox visitation before egg laying, during incubation, and brood rearing. Tarsus length and body mass were measured. Female condition was measured as the residual value of female body mass and tarsus length relationship, and only measurements obtained after the last egg was laid and before the date of first egg hatched of the clutch were used. Egg mass was measured in the same fashion as for the eggs in my study. The results of their study indicated a positive relationship between egg mass and female condition during the incubation period, as high-quality female are able to endure the metabolic costs of incubation, as well as produce larger eggs. A positive correlation was also found between egg mass and nestling size at hatching, but nestling growth was only weakly related to egg size. Smith et al.'s (1993) findings do not support those of my study. One difference between their study and mine is the time at which females were caught and their measurements obtained. I suggest that it may be better to obtain female measurements relating to condition on the date the first egg was laid. Measurements taken at this time could be a better indication of female condition during egg production/laying, for female condition declines during this period, as well as over the course of incubation (Smith et al, 1993). Decreases in female condition, from egg production to egg hatching, may differ between females that begin egg production in higher condition, relative to females that begin egg production in lower condition. Decreases in condition may also vary among females that enter the egg production period with similar condition levels.

In Wendeln's (1997) study of male condition contributing to egg mass in the Common tern (*Sterna hirundo*), he found correlations that confirm that female and male

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condition directly affected egg mass. He found that heavy males mated with heavy females and they produced heavy eggs. These heavy eggs produced larger and more robust offspring, which translated into greater reproductive success. Wendeln (1997) suggests that egg mass is not the only contributor to nestling fledging success; heavy parents must be good at self-provisioning, and their ability to provide nourishment for themselves may enable them to increase their provisioning rate to nestlings.

There are differences between my data collection methods and those of Wendeln's; in determining female condition, I collected weight and tarsus length measurements by capturing adult females, whereas Wendeln used electronic scales placed on known resting sites and mass was recorded and saved by a data logger, as condition was represented by mass only. Another difference regarding female condition measurements is the time during egg laying at which female measurements were obtained. In my study, female measurements were obtained after hatching of the female's clutch, while Wendeln's mass measurements were obtained on the clutch's first egg laying date.

Whittingham et al. (2007) found that female tree swallows did not allocate more resources to eggs laid later in the clutch, as indicated by egg mass. They proposed that environmental conditions play an important role in determining egg mass, specifically that of air temperature and food availability. Females endure fitness costs during egg production that negatively affect their metabolic processes and result in a decline in condition. Warmer temperatures and food abundance may help to negate the trade-off between egg production and female condition. They also stated that individual females

exert an influence on egg mass through heritability of egg size. The heritability of egg size would then favour females that laid larger eggs which males would choose for in order to produce healthier offspring and thereby increasing their reproductive success. They concluded that ambient temperature has the greatest influence on the amount of variation in egg mass within a clutch and female heritability has the greatest influence on egg mass among clutches.

In 2004, Saino et al. published a study on barn swallows (*Hirundo rustica*) that supported a positive connection between egg mass and ambient temperatures. By examining individual eggs within clutches and monitoring the effect that ambient temperature had on egg mass variation for individual females, Saino et al. (2004) found that days of high temperature preceding laying resulted in eggs being heavier than eggs laid after the temperature dropped. They also noted that ambient temperature influenced female condition. They suggested that increases in temperature aid female condition through increasing food availability. Barn swallows are insectivores and increases in temperature increase insect activity. Warmer temperatures also reduce the metabolic costs of egg production to the female. A greater abundance of food, coupled with reduced metabolic stress, could enable females to allocate more resources to eggs, increasing egg mass, while maintaining a higher condition. Whittingham et al. (2007) and Saino et al. (2004) both determined that female condition influenced egg production. However, the influence of female condition was overshadowed by the effects of ambient temperature and food abundance. Ambient temperature and food abundance should be viewed as a confounding variable in these studies, as they directly affect female condition, as well. In

my study, environmental conditions were similar throughout the breeding territories. Therefore, higher temperatures and greater food availability would provide equal benefits to all females and should not have been a factor that impacted female condition. It is likely that the degree to which temperature and food abundance influences female condition differs between 1st and 2nd clutches, so it may be beneficial to separate out 1st and 2nd clutches in future studies.

My prediction that females in better condition would have clutches with a higher mean egg mass and total egg mass was not supported by my findings. Egg mass and female condition were positively correlated, but not in a significant way in my study. This finding could be an artefact of low sample size, or it may be possible that the relationship between egg mass and female condition is species dependent. Confounding variables that may affect egg mass that I did not take into account are ambient temperature, food availability and age. The previously mentioned variables do affect egg mass, therefore egg mass may not signal female quality if she alone is not fully responsible for it.

Condition and egg shell colour.

The prediction that females in better condition will lay eggs with greater blue-green chroma than females in poorer condition was not supported by my findings. No relationship existed between female condition and 1) egg shell hue, 2) UV reflectance of egg shells, 3) egg shell chroma. Numerous studies have described a positive relationship between female condition and blue-green egg colouration (e.g. Lopez-Rull et al., 2008; Moreno and Osorno, 2003; Moreno et al., 2004; Siefferman et al., 2006). There is strong

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experimental and observational support that blue-green egg colouration is an honest indicator of female quality due to the egg production process of depositing biliverdin in egg shells, the possible benefits biliverdin supplies to eggs, and the costs to females during these processes (Lopez-Rull et al., 2008; Moreno and Osorno, 2003; Moreno et al., 2004; Siefferman et al., 2006). In Lopez-Rull at al.'s (2008) study on the variation of egg colour and biliverdin deposition in relation to egg quality and female quality in spotless starlings (*Sturnus unicolor*), they found that females in better condition laid eggs containing greater amounts of biliverdin, resulting in eggs higher in blue-green chroma. Due to the female's ability to endure the cost associated with the removal of biliverdin from her system (the accumulation of free radicals in the body, as biliverdin is an antioxidant), biliverdin deposition in eggs is an honest indication of female quality. In Moreno et al.'s (2004) correlational study of pied flycatchers examining male provisioning, female quality and egg colouration, the offspring from more colourful blue-green eggs received greater paternal care. Offspring from eggs with greater blue-green colouration have also been found to possess better immune systems (Moreno et al., 2005). Morales et al. (2006) examined if the blue-green egg colour of pied flycatchers was related to fledging success and found that females in better condition did lay eggs higher in blue-green colouration. They also found that blue-green colouration was positively associated with nestling immunocompetence.

There have also been studies that did not support a relationship between blue-green egg colouration and female condition. In Hanley and Doucet's (2009) experimental study on ring-billed gulls (*Larus delawarensis*), they examined colouration aspects of

eggs in relation to female quality. They predicted positive correlations between blue-green chroma and female condition, as well as between blue-green chroma and male provisioning efforts. They found slight positive but non-significant relationships between blue-green chroma and each of the two variables. Therefore, blue-green chroma may not be a sexual signal directed at males for the assessment of female quality.

Hanley et al.'s (2008) study of the gray catbird (*Dumetella carolinensis*) examined blue-green chroma in relation to female condition. They predicted that females in better condition would produce eggs higher in blue-green chroma, and that males would provide a higher amount of paternal care to nests containing eggs high in blue-green chroma. There was no significant relationship between female condition and blue-green chroma. An increase in paternal care was however detected in nests that contained eggs high in blue-green chroma.

Hanley and Doucet's (2009) and Hanley et al.'s (2008) studies provided mixed support for blue-green egg chroma being associated with the differential-allocation hypothesis. In Hanley and Doucet's study, differential-allocation was not supported, as blue-green chroma did not significantly induce a greater amount of paternal care (provisioning rate). Hanley at al.'s study did support differential-allocation, as at nests containing eggs greater in blue-green chroma, an increase in paternal care (provisioning rate) was found. It should be noted that different species were observed for each study; ring-billed gulls (Hanley and Doucet, (2009) and gray catbirds (Hanley et al. 2008). These results indicate that blue-green egg chroma may be used as a means of mate assessment by males, but not in all species.

It is widely accepted that birds use UV reflectance in the assessment of potential mates (Cuthill et al., 1999; Prum et al., 2003; Stevens & Cuthill, 2007; Withgott, 2000). The most commonly studied UV signals in birds are those of feather UV reflectance of males influencing female mate choice. Previous studies have also shown a positive correlation between an individual's condition and feather UV intensity (Delhey et al., 2007; Hausmann et al., 2002; Withgott, 2000) A study on tree swallows found that intensely bright UV-reflecting female tree swallows provided greater parental care if mated to intensely bright UV-reflecting males. Additionally, the areas where highly UV-reflecting individuals nested contained a greater abundance of food (Withgott, 2000).

In my study, the majority of the variation in egg shell hue was in the UV component of color although all eggs had negative UV reflectance values, which indicate that starling egg shells elicit low levels of stimulation of ultraviolet cones. While the UV component of egg reflectance does stimulate the avian visual system and elicits a behavioural response (Aviles et al., 2006; Cherry and Bennett, 2001; Hausmann et al., 2002; Withgott, 2000), there is no support for UV reflectance in eggs acting in mate quality assessment, or as a signal of female condition, as was shown in my study. It remains to be determined if cavity-nesting birds are able to differentiate among eggs in a clutch, based on egg colour (Reynolds et al., 2009). Also, it is unknown if males of cavity-nesting birds are able to evaluate the colour of eggs in two different clutches, as would be necessary for the differential allocation hypothesis and the sexually selected egg colour hypothesis to be supported (Reynolds et al., 2009). Future studies on European

starlings could investigate egg colour and the amount of parental care provided by the male.

Investigations have suggested other roles for egg UV reflectance. Aviles et al. (2006) performed a study on UV reflectance's role in egg detectability and predicted that cavity-nesting species would have eggs with greater UV reflectance than eggs of open-cup nesters. They also predicted that egg UV reflectance played a major role in egg detectability and retrieval by parents. In a comparative analysis of 89 species, consisting of 5598 eggs, Aviles et al. (2006) found that cavity-nesting species have eggs with greater UV reflectance than open-cup nesters. Their finding supports the hypothesis that egg UV reflectance is a selected trait for eggs in dark environments (von Haartmann, 1957). Aviles et al. (2006) experimentally manipulated eggs of a cavity-nester (Spotless starling, *Sturnus unicolor*) by removing two eggs from a nest during incubation; one egg was covered with a UV-blocker and the other was covered with horse fat and used as a control. The two eggs were then placed outside the nest and their retrieval was monitored. Control eggs were retrieved more often than the UV blocked eggs, providing support for the prediction that in dimly lit environments, such as cavity nests, egg UV reflectance does provide a benefit in egg detectability and retrieval.

Intraspecific brood parasitism is present in European starlings (Lombardo et al. 1989), but there is a lack of information on intraspecific brood parasitism in relation to the UV component of colour. However, there have been numerous studies that have examined the role of UV eggs shell reflectance as a defense mechanism against interspecific brood parasitism (e.g. Cherry and Bennett, 2001; Spottiswoode et al., 2010;

Lyon, 2007). Cherry and Bennett (2001) suspected that hosts accepted parasitic eggs because the avian visual system could not detect the differences in egg colour, which were clear to human inspection. Spectroscopic analysis of eggs from the parasite, the red-chested cuckoo (*Cuculus solitarius*), and various host species showed that eggs were extremely close in hue (green colour), chroma (green intensity), and UV reflectance. Thus, Cherry and Bennett (2001) speculated that only certain wavelengths are used is assessing egg recognition. Supporting Cherry and Bennett's hypothesis is a study done by Spottiswoode et al. (2010) where they assessed the parasitic relationship between the cuckoo finch (*Anomalospiza imberbis*) and its host, the tawny-flanked prinia (*Prinia subflava*). They concluded that the most important factor in recognizing parasitic eggs is contrast in colour (chroma), including hue and UV. The host species' involved in Cherry and Bennett's (2007) and Spottiswoode et al.'s (2010) studies are open-hole nesters and not cavity nesters, as is my study species. The UV component of egg shell colour may have different roles under different light conditions and among species. Future studies should examine the roles of egg shell UV reflectance, hue, and chroma in relation to intraspecific parasitism in European starlings.

That there are differences in colour perception among species is not a new concept, and it is clearly evident in studies of plumage colouration and mate selection (Ballentine and Hill, 2003; Hill et al., 1994; Roskaft et al., 1986; Santos et al., 2007). To fully understand the meaning of colour and the impact that colour components have on animal behaviour and communication, it is essential to be able to quantify visual data based on receiver specific models (Endler and Mielke, 2005; Maia et al., 2013; Stevens

and Cuthill, 2007; Stoddard and Prum, 2008). However, creating receiver-specific models for spectral data has been difficult to achieve. An unexpected finding of my study was that according to the European starling visual model, egg shells appear yellowish to European starlings, not blue-green, as they appear to our human eyes. This discovery may shed light on the mixed results found in studies of blue-green chroma of egg shells. Studies that have found positive correlations between blue-green chroma and female condition may in fact be correlations between as yet unknown hues and condition. It is also possible that for some avian species, what we see as blue-green also appears blue-green to the bird species, whereas in other species such as the European starling, they appear to be another hue. It would be interesting to conduct the Pavo analysis on the eggs in my study as though the eggs were in an open nest (Pavo contains a background illumination option for analysis under "blue sky") to determine if the yellow colour of eggs is due to the starling visual system or due to the low light conditions within the nestbox.

In my study, a Robinson projection of the starlings' egg shell reflectance spectra showed that the variation in hue among eggs was due to differences in the UV component of colour. Since avian visual systems have four cone types, birds can differentiate among more colours than humans can. Hence, slight variations in colour components may be found to be statistically non-significant, but may in fact be biologically significant to birds. Tools such as Pavo that permit the analysis of variation in colour based on species-specific visual phenotypes have the potential to revolutionize the study of colour, and visual communication and signalling in avian species.

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To conclude, no correlations were found between female condition and either mean egg mass or total egg mass per clutch. Similarly, no correlations were found between female condition and egg shell colour components. However, the tetrahedral colour space and Robinson's projection produced by Pavo indicates that European starlings perceive their eggs as yellow, not blue-green as previously believed. This result underlines and emphasizes the importance of tools, such as Pavo, that enable the analysis of visual cues based on the visual system of the receiver species.

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