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Commentary

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PATERNAL INVESTMENT AND THE "SEXUALLY SELECTED HYPOTHESIS" FOR THE EVOLUTION OF EGGSHELL COLORATION: REVISITING THE ASSUMPTIONS

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THE ADAPTIVE SIGNIFICANCE of bright blue eggs has interested evolutionary biologists for at least a century (Wallace 1889, Underwood and Sealy 2002). Several factors have been proposed as explanations for the evolution of conspicuous eggshell colors, including thermoregulation (Montevecchi 1976, Wink et al. 1985), camouflage (Lack 1958, Oniki 1979), increased visibility to cavity-nesting parents (von Haartman 1957), avoidance of brood parasitism (Victoria 1972), protection against solar radiation (Lahti 2008), and, most recently, sexual conflict within the breeding pair (Hanley et al. 2010). However, the explanation that has received the most attention in the past decade is the "sexually selected hypothesis" of Moreno and Osorno (2003), which was developed to explain the occurrence of blue-green eggs in bird species with biparental care. This hypothesis posits that biliverdin, the antioxidative pigment responsible for the blue-green color of the eggshell, is costly for females to produce and may therefore serve as a reliable indicator of female quality. If so, males should be able to judge the genetic fitness of their mates by the intensity of the coloration of the eggshell, and then adjust their investment in the clutch accordingly. Since the publication of Moreno and Osorno's paper, several experimental studies have attempted to test whether the intensity of eggshell color does, in fact, predict male parental investment.

The majority of these studies (reviewed below) have used a cross-fostering approach to decouple the effects of parental quality and eggshell color, swapping entire clutches of eggs between pairs of nests of approximately the same age and clutch size. Male parental investment is then measured in terms of the frequency of food deliveries to the nestlings, typically several days after hatching. Here, I show that this is an inaccurate measure of paternal investment: it controls for correlations between eggshell color and maternal fitness, but it does not control for correlations between eggshell color and nestling fitness. I discuss several variables that can confound the results of such cross-fostering experiments and recommend ways to improve future studies. I also raise concerns regarding fundamental assumptions of the sexually selected hypothesis, particularly the relationship between paternal care and offspring quality and the heritability of small differences in eggshell color.

The sexually selected hypothesis relies on two assumptions. The first is that the intensity of the blue-green eggshell color is a costly and reliable indicator of maternal quality. This has largely been supported through a series of correlations: although only one study has shown a direct relationship between biliverdin and blue-green eggshell chroma (Moreno et al. 2006a), the intensity of shell coloration has been positively correlated with many maternal traits, including age, body mass, body condition, provisioning rate, and antioxidative capacity (reviewed in Reynolds et al. 2009; but see Cassey et al. 2008, Hanley and Doucet 2009). The second assumption is that high-quality females produce high-quality eggs, because they are able to allocate more costly resources to them. This, too, is fairly well supported: the intensity of eggshell coloration has been shown to be positively correlated with egg volume (Moreno et al. 2004), yolk antibody concentrations (Morales et al. 2006), yolk luteins (Hargitai et al. 2008), and yolk testosterone (López-Rull et al. 2008). These traits, particularly the last, have in turn been linked to several nestling traits that reflect quality and condition, including gape color (Saino et al. 2003), body mass (Schwabl 1996, Quillfeldt et al. 2006), growth rates (Navara et al. 2005), and begging intensity (Eising and Groothuis 2003, Goodship and Buchanan 2006).

Eggshell color, therefore, appears to be correlated with a suite of phenotypic traits that may all be reliable indicators of nestling fitness. If the sexually selected hypothesis is tested by measuring paternal food delivery to nestlings, it is impossible to tell which of these traits—alone or in concert—are actually being used to assess offspring quality. In the Common Canary (*Serinus canaria*),

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TABLE 1. A review of studies that have tested the "sexually selected hypothesis" of Moreno and Osorno (2003) by quantifying male parental investment in relation to eggshell coloration.

Authors	Study species	Controlled for nestling traits?	Supported the hypothesis?
Moreno et al. 2004	Pied Flycatcher (*Ficedula hypoleuca*)	No	Yes
Moreno et al. 2006b	Pied Flycatcher	No	Yes
Krist and Grim 2007	Collared Flycatcher (*F. albicollis*)	No	No
Moreno et al. 2008	Pied Flycatcher	Yes	Yes
Soler et al. 2008	Spotless Starling (*Sturnus unicolor*)	Yes	Yes
Hanley and Doucet 2009[a]	Ring-billed Gull (*Larus delawarensis*)	No	No
Hanley et al. 2008[a]	Gray Catbird (*Dumetella carolinensis*)	No	No
Sanz and García-Navas 2009[b]	Blue Tit (*Cyanistes caeruleus*)	No	Yes
Morales et al. 2010b	Blue-footed Booby (*Sula nebouxii*)	Yes	No
Walters and Getty 2010[b]	House Wren (*Troglodytes aedon*)	No	No

[a] Study was correlative, not experimental, and did not claim to control for either maternal or nestling traits.
[b] Study used the sexually selected hypothesis to test the adaptive significance of brown-patterned (rather than blue) egg.

for example, rates of food delivery depend on the interaction of several factors, including nestling size and position (Kilner 1995), gape color (Kilner 1997), and begging posture (Kilner 2002). Exchanging eggs between sets of foster parents controls for the correlation between eggshell color and maternal fitness, but it leaves open the possibility that nestling quality itself may confound the relationship between eggshell color and paternal investment.

A review of the literature reveals that the majority of studies have not controlled for the confounding correlations between eggshell coloration and other nestling traits, typically because paternal care was measured during the nestling period (Table 1). When these are excluded, only two studies have found a significant relationship between eggshell coloration and paternal investment (Moreno et al. 2008, Soler et al. 2008). These studies provide convincing evidence for the link between eggshell coloration and paternal investment, but it should be acknowledged that this type of experimental support is even more limited than it appears at first glance.

In order to ensure that changes in male provisioning rates are due to eggshell color rather than to confounding nestling traits, future studies should employ one of the many experimental designs that control for such correlations. One option is to measure paternal effort during the incubation period, in terms of nest defense, provisioning to the female, or incubation patterns (e.g., Morales et al. 2010b). For species in which fathers provide little care prior to hatching, nestlings in experimental broods can be re-swapped after hatching to break the correlation between eggshell color and nestling condition (e.g., Soler et al. 2008). Alternatively, Moreno et al. (2008) simply substituted one host egg with an artificial egg (either bright or pale) and subsequently measured food delivery to the host nestlings.

Other assumptions of the sexually selected hypothesis need to be reexamined with equal rigor. Several concerns have already been raised by Kilner (2006), Reynolds et al. (2009) and Cherry and Gosler (2010); to their lists I add two more. First, all of the above-mentioned studies have relied upon the prediction that male parental investment should increase with perceived offspring quality. However, several studies have shown that parents do not always maximize their reproductive output by investing more in high-quality offspring, largely because resource availability and the costs of provisioning influence investment decisions (Clutton-Brock 1991). When food is not limited, parents may deliver food more frequently to low-quality nestlings, presumably in an attempt to compensate for poor condition and increase their chances of fledging (Stamps et al. 1985, Davis et al. 1999, Leonard and Horn 2001). For example, Christe et al. (1996) found that male Great Tits (*Parus major*) made >50% more food deliveries to nests that contained low-mass offspring infested with parasitic fleas than to nests that were free of ectoparasites. In Pied Flycatchers (*Ficedula hypoleuca*)—one of the species commonly used to test the sexually selected hypothesis—Gottlander (1987) found that females were more likely to deliver food to smaller, lower-mass nestlings than to their heavier siblings, and males delivered food to all nestlings equally.

Only under certain circumstances should parents benefit by allocating more effort to high-quality offspring: when resources are limited, such that provisioning is costly, or when low-quality nestlings are in such poor condition that increased parental investment is unlikely to help (Lack 1968, Davis et al. 1999). For example, Bize et al. (2006) showed that Alpine Swifts (*Apus melba*) and European Starlings (*Sturnus vulgaris*) preferentially fed smaller offspring early in the nesting season (when food was abundant), but preferentially fed larger offspring in later nesting attempts (when food was limited). Similarly, Ligon and Hill (2010) found that Eastern Bluebirds (*Sialia sialis*) fed high-quality and low-quality siblings at equal rates under natural conditions, but favored high-quality offspring when the differences between siblings were artificially exaggerated. Parents might also invest more resources in high-quality offspring if the marginal benefits to doing so are exceptionally high; for example, if a slight increase in parental effort brings about a disproportionately large increase in the nestling's prospects of survival and future reproductive value (Lessells 2002). Mock et al. (2005) found that male House Sparrows (*Passer domesticus*) delivered food more frequently to broods that were artificially provisioned, and their mathematical model (parameterized with data from the same population) supported the hypothesis that males should benefit more by increasing investment in the nestlings than by pursuing other activities (such as extrapair copulations).

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Taken together, these studies indicate that a male may either increase or decrease his investment if he perceives an increase in the quality of his nestlings. The direction of the change depends on the costs to the male (in terms of provisioning effort and his future reproductive potential) and the benefits to his offspring (in terms of fitness gains and future reproductive value). These parameters, in turn, are likely to depend on the particular life-history strategy of the study species, along with environmental variables in the study population and even individual characteristics of the fathers themselves (such as age and body condition). Most studies of the sexually selected hypothesis have focused on a small number of temperate, cavity-nesting passerines, relatively short-lived species in which fathers may not benefit from altering their levels of investment in response to small differences in offspring quality. As Cherry and Gosler (2010) noted, the sexually selected hypothesis is more likely to be applicable to long-lived species with extensive paternal care and pair bonds that persist across years, such as seabirds. Future researchers should be careful to ensure that—all other considerations aside—the ecology of their study species is such that fathers are actually predicted to benefit from increasing their investment in a high-quality clutch.

Second, there is a great deal of confusion in the literature as to whether shell color reflects a female's intrinsic genetic quality or her body condition at the time of laying. As Moreno and Osorno (2003) clearly stated in their original formulation of the hypothesis, eggshell color cannot be subject to sexual selection unless it is heritable. It should be repeatable within and across an individual female's clutches, and variance in eggshell coloration should be at least partly attributable to genetic, rather than environmental, variance. Evidence from poultry breeders suggests that eggshell ground color is indeed partly under polygenic control (Punnett 1933, Hutt 1949). However, these early studies quantified broad differences in pigmentation (such as blue vs. white) rather than the fine-scale differences in pigment intensity that are posited to be heritable by the sexually selected hypothesis. Only two studies have examined the repeatability of blue-green eggshell color for females in wild populations, and they yielded mixed results. Collias (1993) found that female Village Weavers (*Ploceus cucullatus*) laid eggs that were repeatable in basic ground color, but not in hue, lightness, or chromaticity. In Pied Flycatchers, by contrast, Morales et al. (2010a) found that four of nine egg color traits were significantly heritable, with heritability accounting for 15–54% of total phenotypic variance.

In seeking support for the sexually selected hypothesis, most researchers have focused on the value of eggshell color as a signal of female body condition, frequently relying on environmental variables and intra-female comparisons to support the relationship. These studies are consistently cited as evidence for the link between female quality and eggshell color, although they essentially confirm the environmental rather than genetic component of its variance. For example, Soler et al. (2008) found that female Spotless Starlings (*Sturnus unicolor*) laid paler eggs when their wing feathers were experimentally clipped, and Moreno et al. (2006a) found that female Pied Flycatchers laid brighter eggs when they were supplemented with additional food. Other authors have found that eggshell color is significantly affected by female age (Siefferman et al. 2006), pollution (Jagannath et al. 2008), rainfall and temperature (Avilés et al. 2007), carotenoid availability (Morales et al. 2011), and the egg's position in the laying order of the clutch (Krist and Grim 2007). These studies support the idea that biliverdin is limited and that shell color is an honest indicator of maternal condition, but they do not support the hypothesis that eggshell coloration is a heritable trait that has evolved through sexual selection.

In summary, several lines of evidence suggest that blue-green eggshell color reliably reflects maternal body condition and reliably predicts nestling body condition. However, few studies have convincingly demonstrated that male birds use eggshell color to assess the genetic quality of their mates. Cross-fostering experiments typically have not controlled for nestling condition, and the sole prediction that these experiments tested—that males invest more care in high-quality offspring—may be applicable only under particular circumstances. Finally, most authors have demonstrated the influence of environmental rather than genetic factors on eggshell coloration.

Future research will benefit from a broader and more rigorous approach to the adaptive value of eggshell coloration, particularly from studies that attempt to simultaneously evaluate multiple competing hypotheses. In order for researchers to correctly test the predictions of the sexually selected hypothesis, they must ensure that the life-history traits of their study species support its assumptions. The most productive studies are likely to come from populations of long-lived, monogamous birds in which a strong relationship between paternal investment and nestling quality has already been demonstrated. Much more information is needed on the extent to which genetic factors control intra-population variation in eggshell coloration, and on the degree to which male birds are able to perceive and judge this variation. Parental investment is likely to be influenced by a combination of several variables, of which nestling quality is only one. Nestling quality, in turn, is likely to be assessed through a combination of several traits, of which eggshell color is only one.

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