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Robin's egg blue: does egg color influence male parental care?

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Abstract A recent hypothesis suggests that birds' blue-green egg colors may be a sexually selected signal of female (and potentially nestling) quality that males use to make parental investment decisions. While there is some empirical support for this idea, both theory and observations question its validity. To test this hypothesis experimentally, we examined the influence of egg color on male American robin *Turdus migratorius* behavior by replacing natural clutches with four artificial eggs that were all either pale or vividly colored, close to the extremes in natural egg coloration. At the end of the incubation period, three unrelated nestlings were fostered into each experimental nest, and parental provisioning behavior was monitored when nestlings were 3, 6, and 9 days old. Male provisioning rate for 3-day-old nestlings was significantly higher in the vivid egg treatment compared to both the pale egg treatment and untreated controls, but there was no effect of egg color on paternal behavior at the older nestling stages. Male feeding rate at unmanipulated nests was only weakly positively related to natural egg color (chroma) when nestlings were 3 days old. These results suggest that blue-green egg color may act as a post-mating signal of female quality or investment in this species, but our findings do not exclude the possibility that egg color pigmentation also serves other adaptive functions.

Keywords American robin · Egg color · Parental care · Mate assessment · Sexual selection · Reproduction

The adaptive significance of avian egg colors has fascinated naturalists (Sorby 1875; Wallace 1889; Poulton 1890) ever since natural selection was first used to explain the characteristics of wild species. Although functional hypotheses such as predation avoidance, structural enhancement, and egg recognition by parents have been successful in explaining some of the interspecific variation in egg colors and patterns, blue-green pigmentation has long defied explanation (Kilner 2006). Moreno and Osorno (2003) and Lahti (2008) have recently suggested two promising—but not mutually exclusive—adaptive explanations for the presence of blue-green pigments in birds' eggshells. First, Moreno and Osorno (2003) suggested that biliverdin, the main determinant of all blue-green egg colors, might be a signal of female condition that males attend to when adjusting their parental investment. Second, Lahti's (2008) hypothesis suggested that biliverdin in eggshells absorbs and reflects solar radiation that could otherwise harm the developing embryo. This could help explain the low concentrations of biliverdin in many white-colored eggs, but does not rule out other adaptive roles for this pigment. Hanley et al. (2010) also suggested that egg color might "blackmail" males into providing more incubation, or more incubation-feeding to the female, so that eggs are exposed less to potential predators. This hypothesis is relevant only

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to those species in which males actually provide these services.

The sexually selected egg color hypothesis (SSEC; Moreno and Osorno 2003) requires (a) that the intensity of blue-green eggshell color is an honest signal of female and potentially offspring quality, (b) that variation in egg color is detectable by birds, and (c) that males gain a fitness advantage by adjusting their investment in response to that variation. Certainly, blue egg color is variable within species (Moreno et al. 2005; Siefferman et al. 2006; Cassey et al. 2009) and is well within the bird-visible spectrum (Burkhardt and Finger 1991). A recent experiment also demonstrated that birds can discriminate among experimental eggs that span the natural range of variation in color (Soler et al. 2008). Finally, egg color can be readily observed by the male parent whenever the female is off the nest, even if the male does not incubate.

Moreno and Osorno (2003) also argued that, because it has antioxidant properties (Kaur et al. 2003), biliverdin would be valuable to the female and thus its deposition into eggshells potentially costly. Therefore, only high-quality females should be able to deposit large quantities of biliverdin in their eggshells. Female gray catbirds (*Dumetella carolinensis*), for example, laid bluer eggs when they had higher antioxidant levels in their bloodstream (Hanley et al. 2008). In the European pied flycatcher (*Ficedula hypoleuca*), a cavity-nesting songbird with pale blue eggs, females that laid the bluest eggs had lower post-laying antioxidant levels if they were stressed before egg laying (Morales et al. 2008).

Correlational studies have also supported the assumptions of the SSEC hypothesis by linking the intensity of blue-green coloration with female body condition in European pied flycatchers (Moreno et al. 2004, 2005), collared flycatchers (*Ficedula albicollis*; Krist and Grim 2007), and Eastern bluebirds (*Sialia sialis*; Siefferman et al. 2006), all cavity nesters with pale blue eggs. Moreover, in European pied flycatchers, the vividness of blue-green eggshell color is also positively correlated with female immunocompetence, maternally derived antibodies in the yolk, nestling immunocompetence, and fledging success (Moreno et al. 2005; Morales et al. 2006). A decrease in egg color intensity through the laying sequence also suggests that biliverdin is limited in that species (Moreno et al. 2005), making it a plausible mechanism for honest signaling.

Despite the apparent support for the SSEC, it remains controversial (Reynolds et al. 2009). One survey of intra- and inter-clutch variation in egg color in the Muscicapoidea suggests that there is so little intraspecific variation that birds may not be able to use variation in egg color to discriminate among clutches (Cassey et al. 2009). Moreover, there was no consistent relation between blue-green egg color and measures of maternal egg investment in two of those species (*Turdus merula* and *Turdus philomelos*) in New Zealand (Cassey et al. 2008). Similarly, in the spotless starling (*Sturnus unicolor*), blue-green egg color did not accurately predict female or egg quality despite both being positively correlated with eggshell biliverdin (López-Rull et al. 2008). Nonetheless, in another experimental study using the same species and controlling for female and nestling characteristics, paternal feeding rates increased significantly with more vivid blue-green artificial eggs (Soler et al. 2008). Likewise, cross-fostering experiments that decoupled female characteristics from egg color in European pied flycatchers found a positive correlation between egg color and paternal nestling feeding rates (Moreno et al. 2006), though not in collared flycatchers (Krist and Grim 2007).

To date, experimental tests of the SSEC hypothesis have yielded equivocal results, but almost all studies have focused on cavity-nesting birds with pale blue eggs, where variation in egg color is slight and egg color might be hard to detect inside a darkened nest cavity. Thus, in the present study, we tested the key prediction of the SSEC hypothesis—that egg color influences paternal investment—in an open-cup nesting species with vivid blue-green eggs, the American robin (*Turdus migratorius*). Variation in the intensity of egg coloration is quite noticeable within our study population. Since humans are not predicted to be able to discriminate colors as well as birds (Cassey et al. 2009), we assumed that robins could discriminate among these egg colors as well. Using artificial eggs representing extremes in this natural color variation, we experimentally decoupled egg color from female and nestling quality and looked at paternal investment while controlling for other factors.

Methods

Study sites

In April–August 2008, we surveyed dozens of rural and residential properties within 100 km of Kingston, ON, Canada (42° N, 76° W) to find nesting pairs of robins. The highest robin densities and therefore most nests sampled were on or <100 m from human-made structures near lawns, fields, and gardens.

Egg color manipulation

Natural robin egg color varies from a relatively pale sky blue to a rich turquoise (Fig. 1a). Artificial eggs were hand-crafted to typical egg volume and shape (Sallabanks and James 1999) using a measured mass of wet clay (Fig. 1a) and painted to match natural robin eggs as closely as possible based on reflectance spectra (Fig. 1b), using commercially available acrylic paint (satin finish interior/

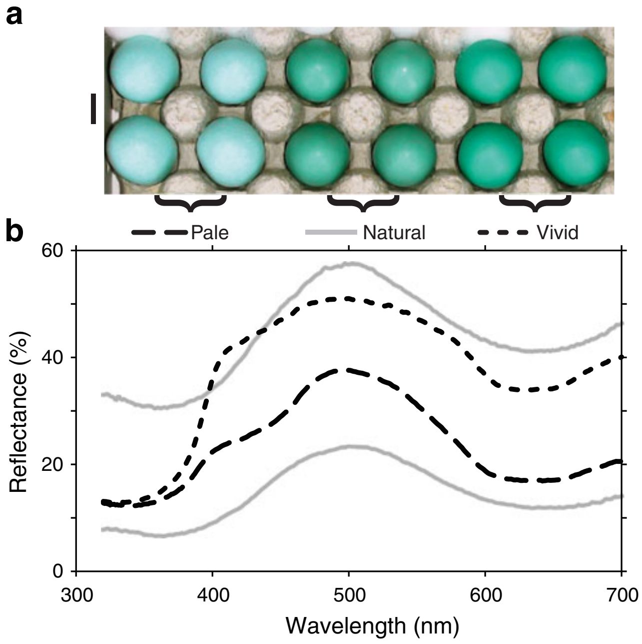

Fig. 1 American robin egg color: **a** natural (*center*) and artificial clutches of four eggs each (*scale bar on the left* is 10 mm long), **b** reflectance spectra from natural and both pale and vivid artificial clutches; *gray lines* indicate the range of reflectance spectra from eggs (n=448) in natural clutches (n=113), showing the eggs with the lowest and highest brightness in this sample

exterior MF Porticobase D; Parade of Paints, Kingston, ON, Canada) and various pigments. The dried clay eggs (11.70–12.07 g, n=20) weighed more than natural eggs (5.44–8.28 g, n=450) and were close to the extremes in natural coloration but did not reflect in the UV (Fig. 1b). All females resumed incubating the artificial eggs within minutes after we left the nest vicinity.

For each experimental treatment, we used three synchronous nests within a few kilometers of each other that were located on, or prior to, their second full day of incubation. We required three synchronous nests for each experimental manipulation because high predation rates meant that more than one possible source nest was required to ensure the availability of foster nestlings of the correct age. The natural eggs of the most accessible nest in each triad (clutch sizes 3–5, mean 3.83, n=38) were collected and replaced with four clay eggs, all painted either pale or vivid blue-green (Fig. 1a). All nests whose eggs were not replaced were monitored for natural variation in both egg traits and parental provisioning.

We visited each nest every 2 to 3 days to determine egg-laying and hatching dates, by candling eggs when necessary. Natural clutches were replaced with artificial eggs ≤2 days after clutch completion. When the first natural egg would have hatched, artificial eggs were replaced with three <2-day-old foster hatchlings from another nest. We put three nestlings in each nest, rather than four, both because source broods of four were not always available and to prevent brood reduction from complicating our analyses, since such reduction is much less likely with brood size three (unpublished data, this study).

Of 86 unmanipulated clutches that we followed until failure or fledging, 40 fledged young, 33 were preyed upon (n=19 at the egg stage, 14 as nestlings), and 13 were abandoned due to broken eggs or human disturbance. Of 27 experimental broods (15 vivid, 12 pale) containing three foster nestlings, only 13 (eight vivid, five pale) survived until the nestlings were 3 days old and thus had parental feeding visits recorded.

Measurement of egg color

The reflectance spectra of all artificial eggs, as well as the natural eggs in all nests, were measured at five haphazardly chosen locations on the egg surface, using Ocean Optics (Dunedin, FL, USA) equipment: USB4000 UV-VIS spectrometer, a PX-2 Pulsed Xenon lamp, a fiber optic cable and probe (P400-2-UV-VIS), and SpectraSuite software. The reflectance spectra of robin eggs are characterized by a peak at about 500 nm (Fig. 1b)—that we perceive as blue-green—corresponding to the hue of biliverdin (Falchuk et al. 2002). In this study, we used two measures of spectral purity in our analyses: blue-green chroma (BGC), which focuses on the blue-green portion of the spectrum (415–585 nm), and a measure of chroma (CHR) based on segment classification (Endler 1990), which gives a general measure of spectral purity that is sensitive to the shape of the entire reflectance curve in the bird-visible region. For curves of a similar shape, these indices estimate the relative vividness of the eggshell color; lower values correspond to both paler and muddier colors (Endler 1990).

We calculated BGC as the proportion of total reflectance (luminance) that falls in the 415–585-nm range ($\mathrm{BGC}=R_{415-585}/R_{320-700}$) and chroma as $\mathrm{CHR}=\left[\left(R_r-R_b\right)^2+\left(R_g-R_u\right)^2\right]^{0.5}$, where the subscripts refer to different segments of equal range in the bird-visible spectrum (r=605–700 nm, b=415–510 nm, g=510–605 nm, u=320–415 nm; Montgomerie 2006). CHR and BGC are not significantly correlated in our sample of natural clutches ($r=-0.23$, P=0.16, n=38) and thus measure different aspects of egg coloration. Mean clutch CHR and BGC of vivid and pale artificial eggs were significantly different, and significantly different from natural eggs, except with respect to BGC of natural and vivid artificial eggs (Table 1).

Parental investment

Adults were captured using mist nets placed near their nest and were marked individually with a locally unique combination of two color bands and a metal band. Females

Table 1 Chroma indices CHR and BGC measured from clutches of natural ($n=38$) and both pale ($n=6$) and vivid ($n=7$) artificial eggs

Egg type	CHR	BGC
Natural	15.03±14.33–15.72	0.551±0.546–0.555
Artificial-PALE	25.85±23.15–28.56	0.511±0.502–0.520
Artificial-VIVID	17.87±16.23–19.52	0.546±0.530–0.562

Values are means ± 95% CI of clutches with three to five eggs measured per clutch

tend to have paler head plumage than males (Sallabanks and James 1999), but sex was confirmed by presence/absence of a brood patch, which is present only on females.

Nestling provisioning by the parents was video-recorded when the nestlings were 3 days [mean (95% CI): experimental, 3.24 days (3.00–3.49), $N=13$; unmanipulated, 2.90 days (2.65–3.14), $N=34$], 6 days [experimental, 6.37 days (5.87–6.87), $N=9$; unmanipulated, 5.83 days (5.61–6.05), $N=37$], and 9 days old [experimental, 9.37 days (9.05–9.70), $N=9$; unmanipulated, 8.87 days (8.58–9.15), $N=27$]. High definition video cameras (DCR-SR100 HDD Handycam; Sony, San Diego, CA, USA) were placed about 5 m from each nest beginning 1–5 h after sunrise [experimental, 3.42 h (2.80–4.04), $N=31$; unmanipulated, 3.29 h (3.02–3.55), $N=98$].

Videos were reviewed using Sony Vegas Platinum 8 software. Both the number of visits where at least one nestling was fed and the total time each adult was present at the nest were calculated as an hourly rate for each parent. All experimental nests contained three nestlings, while unmanipulated nests contained one to four nestlings ($n=98$).

Statistical analysis

We analyzed our comparatively large sample of unmanipulated nests to estimate population characteristics, using hierarchical partitioning (Quinn and Keough 2002) to assess which variables might best predict the provisioning rates of each parent. We used several potential explanatory (predictor) variables that have been found, or might be expected, to influence provisioning of songbird nestlings: feeding rate of the other parent, female time at the nest, time of day, ambient air temperature, average age and number of nestlings, average egg date for the clutch, and the number of previous nesting attempts known or suspected to have occurred for each pair. Parental feeding rates were log-transformed to normalize residuals.

Variables determined to be important by hierarchical partitioning (Quinn and Keough 2002) for each parent were included, along with egg color treatment, in full models of parental feeding behavior at the experimental nests. This full model was used to test for the significance of egg color treatment while controlling for all predictors that had a significant influence on the feeding rates of each parent at unmanipulated nests. Given the small sample sizes for our experimental treatments, this full model ensured that variation in variables that were influential at unmanipulated nests was controlled when assessing any treatment effect. We then used an information theoretic (IT) approach (Anderson 2008) to evaluate the fit of the full model and simpler models to the data. With this approach, models are ranked by corrected Akaike information indices (AICc) from best to worst; model probabilities (weights) indicate the probability that each model is correct, given the data; and evidence ratios provide an estimate of the relative strength of evidence of each model compared to the best model in the set (see also ESM).

All statistical analyses were performed with R 2.10.0 (R Development Core Team 2009), using add-on packages hier.part (version 1.0-3) for the hierarchical partitioning and MuMIn (v. 0.12.2) for information theoretic model evaluation. For hypothesis testing, alpha was set at 0.05.

See online supplement (ESM) for further details on study species, measuring egg color, identifying adults, video recording, and statistical analyses.

Results

Natural parental provisioning behavior

Parental feeding visit rates were successfully recorded at 40 unmanipulated nests: 33 on nestling day 3, 37 on day 6, and 27 on day 9, resulting in 98 sample bouts where both parents' feeding visit rates were recorded (on all 3 days at 20 nests, on 2 days at 17 nests, and on only 1 day at three of the nests).

Hierarchical partitioning analysis showed that mean nestling age, the number of chicks, and sex of parent, as well as the amount of time that the female spent at the nest and its interaction with the number of chicks, were potentially important predictors of parental feeding visit rates. A model containing all of those variables (Table 2) was the highest ranked model using the IT approach and was well supported (weight=0.89). No other model was as well supported (ΔAICc<2), given the data (ESM Table 2). At unmanipulated nests, the male fed significantly more frequently than the female (Table 2), controlling for the other variables—male feeding visit rates were greater than or equal to those of the female in 86 of the 98 paired comparisons. Also, feeding visit rates of both parents increased significantly with both nestling age and number of chicks (Table 2). Females often made additional (non-provisioning) visits, mostly to brood nestlings, averaging 2.54 such visits per hour on nestling day 3 ($n=33$ nests), 1.81 on day 6 ($n=37$), and 1.70 on day 9 ($n=27$). Thus, the

Table 2 General linear mixed model predicts nestling feeding rates (n=194 samples bouts at 40 unmanipulated nests) with nest as a random factor to account for repeated measures of each brood (sampled at nestling ages 3, 6, and 9 days)

Parameter	Estimate	95% HPD	*t*	*P*
Intercept	−0.21	−0.43–0.03	1.8	0.07
Age of chicks (days)	0.02	0.007–0.03	3.3	0.001
Sex of parent	0.17	0.12–0.21	7.8	<0.0001
No. of chicks	0.21	0.13–0.22	6.4	<0.0001
Female time at nest (min/h)	0.007	0.001–0.012	2.4	0.02
No. chicks×female nest time	−0.003	−0.005 to −0.001	3.1	0.002

Estimates for each parameter are shown with highest probability densities (equivalent to confidence limits) and *P* values calculated by Markov–Chain Monte Carlo sampling

total time spent by the female at these unmanipulated nests also decreased from an average of 39 min/h on days 3 to 23 min/h on day 9, even though her feeding visit rate increased.

Males rarely visited the nest without food and were never observed brooding. As a result, the total time that males spent at the nest averaged only 5.9 min/h on day 3, declining to 3.2 min/h on day 9. Although males were occasionally observed coming to the nest while the female was brooding, they more often arrived shortly after her departure and thus may have delayed a feeding visit when she was on the nest. Despite this, the male made more feeding visits when the female spent more total time feeding and brooding (Table 2).

To simplify and increase the statistical power of further analysis of male provisioning rates, we performed a separate analysis for each nestling age (3, 6, and 9 days), using the predictors described above (no. of chicks, female time at nest, and the interaction term). Full models at each nestling age explained ≥40% of the variation in male feeding rates.

Parental responses to egg color manipulation

While males could have seen their mate's natural eggs for up to 4 days during egg laying, the mean colors (BGC and CHR) of eggs in the natural clutches of nests in the vivid (n=8) and pale (n=5) egg color treatments were not significantly different (Wilcoxon tests, P>0.50 for each color variable). Thus, natural egg color should not have biased parental feeding visit rates in these treatments.

Of the 13 experimental clutches (eight vivid, five pale) that had three nestlings survive to 3 days old, only nine (five vivid, four pale) still had three nestlings survive to ages 6 and 9 days. Total female time at the nest did not differ significantly between egg color treatments (Table 3) at any nestling age. Because nestlings were slightly older in vivid egg nests at all three nestling ages (and significantly older on day 6; Table 3), we included actual mean nestling age in subsequent analyses.

On nestling day 3, males provisioned significantly more frequently at nests with vivid eggs (Table 3; Fig. 2a). Similarly, egg color treatment (pale vs vivid) was significant in the full model (Table 4) predicting male feeding visit rate and was included in all four of the highest ranked models (ΔAICc<6; ESM Table 3). The best model included only egg color treatment and the amount of time that the female spent at the nest per hour as predictors and was well supported (weight=0.69), and the strength of evidence for this model is about 20× that of the highest ranked model that does not include egg color treatment (ESM Table 3). In the best model, male feeding visit rate in the vivid egg treatment (least squares mean=5.38 visits per hour, 95% CI=4.44–6.48, n=8) was 1.8 times that in the pale egg treatment (2.93 visits per hour, 95% CI=2.21–3.81, n=5). Interestingly, this difference is due only to an increase in male provisioning at nests with vivid eggs, as male provisioning rates at pale egg nests were very similar to those at unmanipulated nests with three 3-day-old nestlings (mean=2.67 visits per hour, 95% CI=1.72–3.62 visits per hour, n=10 nests). Female provisioning rates were also much higher at nests with vivid eggs (Table 3). Thus, a model with only egg color treatment and female provisioning rate (log-transformed) as predictors is also significant (R^2=0.49, F=4.7, P=0.036, df=2, 10), but female provisioning rate does not make a significant contribution to that model (t=0.8, P=0.43). Moreover, even when controlling for the female's provisioning rate and time spent at the nest, male provisioning rate was significantly higher at nests with vivid eggs.

On nestling days 6 and 9, both female and male feeding visit rates at experimental nests were not significantly influenced by egg color treatment (Table 3; Fig. 2)—the ratio of male provisioning rates at vivid and pale egg treatments was 1.07 and 1.20 at nestling ages 6 and 9 days, respectively.

Parental responses to natural egg color variation

Having found a significant effect of egg color on male feeding visit rates when nestlings were 3 days old, we looked for the effects of egg color on parental feeding rates at the 40 unmanipulated nests. To do this, we analyzed models of male provisioning rate at each nestling age, with female time at the nest, the number of chicks, and the interaction term (as above) as predictors, as well as both BGC and CHR in separate analyses.

For 3-day-old nestlings, there is only weak positive relation between male provisioning rate and CHR (Fig. 2), though that relation was significant before removal of the

Table 3 Comparison of pale and vivid clutch treatments: parental provisioning rates and variables identified as potentially important predictors of male provisioning rates at unmanipulated nests

Variable	Day 3			Day 6			Day 9		
	Vivid (8)	Pale (5)	Test	Vivid (5)	Pale (4)	Test	Vivid (5)	Pale (4)	Test
Female time at nest (min/h)	30.5	35.7	*W*=16	26.2	36.6	*W*=3	23.8	15.3	*W*=12
	23.5–35.3	27.5–47.3	*P*=0.62	17.9–36.1	31.4–41.2	*P*=0.11	10.3–37.4	10.5–20.0	*P*=0.73
Mean nestling age (day)	3.3	3.2	*W*=22	6.8	5.8	*W*=20	9.6	9.1	*W*=17
	2.8–3.5	3.0–3.5	*P*=0.82	6.5–7.3	5.7–5.9	*P*=0.02	9.3–9.8	8.8–9.5	*P*=0.10
Female provisioning rate (visits per hour)	3.7	1.6	*W*=33	2.9	2.3	*W*=14	3.5	3.3	*W*=11
	2.7–4.9	0.6–3.5	*P*=0.07	2.4–3.3	1.2–3.0	*P*=0.41	2.0–4.9	2.8–4.2	*P*=0.90
Male provisioning rate (visits per hour)	5.34	3.23	*W*=35	4.04	3.77	*W*=11	4.14	3.44	*W*=12
	4.4–6.4	2.3–4.0	*P*=0.03	2.4–5.2	2.4–4.7	*P*=0.90	2.3–5.3	2.6–4.3	*P*=0.73

Data are means and bias-corrected 95% CIs (BCa). Wilcoxon tests compare vivid and pale egg treatments; sample sizes in parentheses

outlier (ESM Figure 1). Moreover, there is only weak support (weight=0.33) for the best model that includes CHR (Table 4) and little support (weight=0.14) for the best model that includes BGC. In the full model, the relation between male provisioning rate and CHR is positive but not significant (Table 4). For nestling ages 6 and 9 days, there is little support (weight<0.2) for any of the models containing either color variable (ESM Table 4) and neither of the relations between male provisioning rate and CHR is significant when controlling for other variables (Fig. 2).

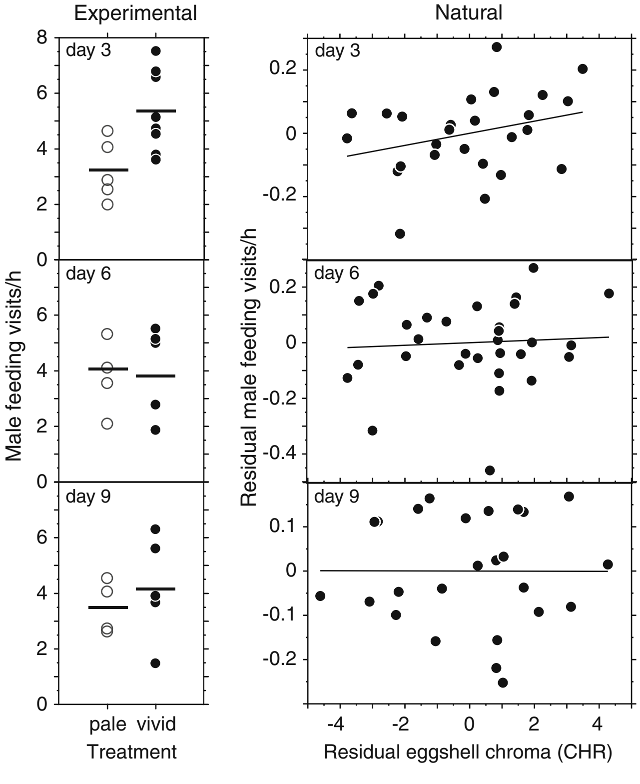

Fig. 2 Male provisioning rates for nestlings at age 3, 6, and 9 days relative to (*left*) egg color treatment (pale, vivid) at experimental nests and (*right*) eggshell chroma (*CHR*) at natural, unmanipulated nests (partial residual plots control both CHR and male provisioning rate for the amount of time the female spent at the nest, the number of chicks, and the interaction between these two predictors). See also ESM Fig. 1 for details of an outlier that was removed from the analysis of 3-day-old nestlings in natural broods

Discussion

In this study, we provide a clear, experimental demonstration that male American robins adjust their nestling provisioning rates in response to the vividness of the

Table 4 Full models to predict male provisioning rates when nestlings were 3 days old in relation to egg color at experimental (all with brood size=3) and natural, unmanipulated nests, where egg color in experimental clutches was either vivid (solid dots, *n*=8; see Fig. 2) or pale (open circles, *n*=5; see Fig. 2) or in natural clutches (*n*=40) was measured as chroma, averaged over the whole clutch

	Estimate	95% CI	*t*	*P*
Experimental nests				
Intercept	0.56	0.06–1.06	2.5	0.03
Egg color treatment	−0.21	−0.33 to −0.09	3.9	0.003
Mean actual nestling age (days)	0.01	−0.13–0.16	0.23	0.82
Female time at nest (min/h)	0.006	0.001–0.01	2.3	0.05
Unmanipulated nests				
Intercept	−1.4	−2.7 to −0.14	2.3	0.03
CHR (chroma)	0.02	−0.007–0.05	1.5	0.14
No. of chicks	0.57	0.25–0.89	3.7	0.001
Female time at nest (min/h)	0.04	0.008–0.07	2.7	0.01
Female nest time×no. chicks	−0.012	−0.02 to −0.004	3.1	0.006

blue-green color of their mate's eggs, consistent with the SSEC (Moreno and Osorno 2003). Male robins who saw more vividly colored artificial eggs in their nest fed 3-day-old nestlings almost twice as often as those who saw pale eggs, controlling for other variables (Fig. 2). Our experiment was designed to isolate the effect of egg color from the quality of both females and nestlings, and as a result, despite small sample sizes, the effect of the treatment was large and statistically significant. We also controlled statistically for other variables identified separately as influencing about half of the variation in male provisioning rates at unmanipulated nests in the same populations.

Only one other study, on the spotless starling, a cavity-nesting species with pale blue-green eggs, has found similar experimental support for the SSEC hypothesis (Soler et al. 2008). That study also employed artificial eggs and foster nestlings to remove any link between egg color and both female quality and nestling vigor. On nestling day 4, spotless starling male provisioning rate at nests that had artificial "dark" eggs was about twice that at "pale" nests (Fig. 4 in Soler et al. 2008), similar to what we found when American robin nestlings were 3 days old (Fig. 2a).

Our study raises at least two interesting questions about male provisioning rates: (1) why was the influence of egg color not detected at later nestling ages (6 and 9 days old) and (2) why was there only a weak effect of egg color at unmanipulated nests? In the spotless starling, there was increasing overlap in the effect of egg color treatments as nestlings aged (Fig. 4 in Soler et al. 2008), but the difference between male provisioning rates at pale- and dark-egg nests remained quite large and significant until the nestlings were 15 days old. In American robins, there was no appreciable effect of egg color on male provisioning rates by the time nestlings were 6 days old (ESM Table 4). Our results from natural clutches also mirror this pattern (Fig. 2), showing no correlation between egg color and male provisioning rates when nestlings were 6 and 9 days old. Paternal effort and egg color were positively correlated at unmanipulated clutches when nestlings were 3 days old, but that relation was weak and not statistically significant (Fig. 2; Table 4).

Soler et al. (2008) replaced newly laid eggs with artificial eggs every day during the egg-laying period, so that male parents had little opportunity to see natural eggs and thus to use that cue of female quality. We replaced full clutches of American robins as soon as egg laying was finished, so males could have seen freshly laid eggs for four or more days. It is possible, therefore, that male robins in our study may have perceived mixed signals when assessing female quality and thus used offspring quality and begging intensity to adjust their provisioning rates as their nestlings aged. It is also possible that the shorter nestling periods, higher feeding rates, and high predation risk experienced by open nesting species relative to cavity-nesting species may increase the importance of audible hunger signals at older nestling ages. Indeed, a declining effect of egg color on male feeding visit rates might be expected if begging intensity becomes a more important predictor of offspring quality and needs for paternal provisioning as nestlings age (Smith and Montgomerie 1991).

Several other studies have also reported correlations between male provisioning rate and the intensity of blue-green egg color. However, only two of these have looked at correlations between egg color and male feeding rates in a completely natural context. Moreno et al. (2004) found significant correlations between male provisioning rates and two chromaticity indices of eggshell color in the European pied flycatcher, indicating that males fed more often at nests where egg color was a deeper, more saturated blue. In gray catbirds, Hanley et al. (2008) found a strong positive relation between male feeding rate and average blue-green chroma of the clutch, controlling for female provisioning rates. In addition, two egg cross-fostering studies have also looked for correlations between provisioning rates and egg color. In the European pied flycatcher, there was a significant positive correlation between the proportion of feeding visits provided by the male and both the maximum and the standard deviation of egg blue-green chroma in a clutch (Moreno et al. 2006), but no such correlation with the mean clutch blue-green chroma. In the collared flycatcher, there was also no relation between male provisioning rates and mean clutch blue-green chroma of natural eggs (Krist and Grim 2007).

The absence of a strong correlation between male provisioning rates and egg color at unmanipulated nests, especially in light of our experimental results, is somewhat puzzling. Possible explanations include (a) that we did not quantify an aspect of natural egg color that parent's actually attend to, (b) that male provisioning rates at natural nests were influenced by other variables (e.g., weather, habitat, clutch size, laying date, paternity) that should be controlled statistically, or (c) that egg color serves other purposes in addition to signaling female quality. Certainly many methods have been used to quantify egg color (ESM Table 1), and it is not clear that all indices are equally effective at capturing the variation that males attend to as a signal of female quality. It is possible, for example, that the color of the egg at the blunt pole is most important for egg discrimination, as has been shown in potential hosts of obligate brood parasites (Polačiková and Grim 2010). We clearly need some experimental work to determine what blue-green egg color traits birds can discriminate and remember.

While a weak correlation between male provisioning rates and egg color supports the SSEC hypothesis, other adaptive (and non-adaptive) explanations for the blue-green color of

American robin egg cannot be ruled out. For example, blue-green pigmentation due to biliverdin might sometimes be cryptic (Underwood and Sealy 2002; Langmore et al. 2009), may provide some protection from solar radiation (Lahti 2008), or could help to strengthen the eggshell (Solomon 1997). These potential roles for biliverdin in the eggshell have so far received the least attention and provide some interesting possibilities for further discovery.

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