

Egg color as an adaptation for thermoregulation

David Westmoreland,^{1,4} Matthew Schmitz,² and Kevin E. Burns³

¹Department of Biology, HQ USAFA/DFB, 2355 Faculty Drive, Suite 2P389, US Air Force Academy, Colorado 80840, USA

²Department of Orthopaedic Surgery, 2200 Bergquist Drive Suite 1, Wilford Hall Medical Center, Lackland AFB, Texas 78236, USA

³Department of Mathematical Sciences, HQ USAFA/DFMS, 2354 Fairchild Drive, Suite 6D124, US Air Force Academy, Colorado 80840, USA

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ABSTRACT. Avian embryos are incubated at temperatures only 2–6 °C below that at which hyperthermia begins to influence survival. In habitats where sunlight directly strikes the eggs, even for short periods, heat gain may be a substantial threat to survival, and reflective pigmentation may reduce the rate of heat gain. The results of previous studies suggest that light-colored eggs acquire heat slower than dark eggs, but artificial pigments were used to create differences in egg coloration. This approach is problematic because natural eggshell pigments have low absorbance in the near-infrared waveband that encompasses about half of incident solar radiation. We used naturally-pigmented eggs to measure the influence of egg coloration on heat gain. Triads ($N = 18$) of eggs from Brewer's (*Euphagus cyanocephalus*), Red-winged (*Agelaius phoeniceus*), and Yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds were crossed with six nests of each species and either exposed to full sunlight or placed under a diffusing umbrella. Thermistors recorded internal egg temperature every minute until an asymptotic temperature was reached. Eggs in full sunlight acquired heat more rapidly than eggs in the shaded environment, but heat gain did not vary with egg color in either environment. Eggs placed in Yellow-headed Blackbird nests took longer to reach asymptotic temperature, but there was no significant egg-by-nest interaction. Thus, it appears that differences in reflectivity of eggshell pigments in the visible range (400–700 nm) do not result in different rates of heat acquisition. The thermoregulation hypothesis was not supported.

SINOPSIS. El color de los huevos como una adaptación para la termoregulación

Los embriones de las aves son incubados a temperaturas entre 2–6 grados centígrados bajo el grado de hipertemia en donde se puede influir en la sobrevivencia. En habitats en donde la luz le da directamente a los huevos, aunque sea por periodos cortos, la ganancia en calor puede ser de gran peligro para la supervivencia y la pigmentación pudiera reducir la ganancia de calor. Los estudios previos sugieren que los huevos de colores claros absorben calor más lentamente que los huevos oscuros. Este método de acercamiento es problemático porque los pigmentos naturales en los cascarones tienen baja absorvancia cerca del infrarojo, lo que armoniza con cerca de la mitad de la incidencia de la radiación solar. Utilizamos huevos naturalmente pigmentados para medir la influencia de la coloración de los huevos en la ganancia de calor. Trios ($N = 18$) de huevos de *Euphagus cyanocephalus*, *Agelaius phoeniceus*, y de *Xanthocephalus xanthocephalus*, fueron entrecruzados con seis nidos de cada especie, ya sea expuestos totalmente a la luz o colocados en luz difusa bajo una sombrilla. Utilizamos termistores para tomar la temperatura interna de los huevos en lapsos de minutos hasta que alcanzaran un punto de temperatura asintótica. Los huevos a plena luz absorbieron calor más rápidamente que los huevos en ambientes sombreados, pero la ganancia en calor no varió en armonía con el color de los huevos en los diferentes ambientes. Los huevos colocados en los nidos de *Xanthocephalus* tomaron más tiempo en alcanzar una temperatura asintótica, pero no hubo una interacción significativa entre los huevos por nido. Parece ser que las diferencias en reflectividad en la pigmentación de los cascarones, en el espectro de luz visible (400–700 nm) no arroja como resultado diferencias en la tasa de ganancia de calor. Los resultados no apoyan la teoría de termoregulación.

Key words: blackbirds, egg color, egg temperature, pigmentation, thermoregulation, Icteridae

Biologists have traditionally argued that the function of avian egg coloration is camouflage (Darwin 1859, Wallace 1890, Cott 1940, Lack 1958). As Skutch (1976) noted, however, the

eggs of passerines “. . . rarely match the color of the nest lining. . . and seem to vary in shade without rhyme or reason.” Noncryptic egg coloration may be explained by selection pressures that favor bright coloration, such as nest parasitism, female signaling, or egg thermoregulation. Nest parasitism selects for high interclutch variation in color to curtail the evolution of mimicry by

⁴Corresponding author. Email: David.Westmoreland@usafa.af.mil

nest parasites (Moller and Petrie 1991, Oien et al. 1995, Stokke et al. 1999). Selection for female signaling favors deposition of the blue-green pigment biliverdin on the egg surface that advertises high antioxidant capacity in the female (Moreno and Osorno 2003, Moreno et al. 2004, Soler et al. 2005).

Thermoregulation as an explanation for bright egg coloration may generally apply to open-nesting species, but has received little experimental investigation. By reflecting incident sunlight, lightly pigmented eggs might protect embryos from hyperthermia when adults are away from the nest (Montevecchi 1976, Bertram and Burger 1981). Incubated eggs vary in core temperature from 34° to 38° C, and temperatures above 40° C place embryos at risk of mortality (Bennett and Dawson 1979, Lewin 1988, Burley and Vadehra 1989). Thus, solar heating could be a substantial and common threat to survival. The thermoregulation hypothesis has received support from studies of domestic chickens (*Gallus gallus domesticus*; Montevecchi 1976) and Ostriches (*Struthio camelus*; Bertram and Burger 1981) eggs. However, because the authors used artificial pigments to darken eggshells, the applicability of the results of these studies to natural eggs is questionable. Regardless of color, avian eggshell pigments have low absorbance in the near-infrared range (Bakken et al. 1978). Because about half of incident sunlight falls within this range, solar heating of eggs may be unrelated to egg color even during direct exposure to solar radiation. In addition, many birds with lightly pigmented eggs nest in shaded habitats where protection from solar radiation would seem unnecessary.

Our objective was to determine whether eggs that differ in coloration acquire heat at different rates. Although such an effect seems unlikely, a test of the thermoregulation hypothesis is needed. We tested this hypothesis by comparing rates of heat acquisition among differently-pigmented eggs of three species of blackbirds (Icteridae).

METHODS

Study species. We studied the eggs and nests of blackbirds (Icteridae) that differ in egg pigmentation and nest structure: Brewer's Blackbird (*Euphagous cyanocephalus*), Red-winged Blackbird (*Agelaius phoeniceus*), and Yellow-headed

Blackbird (*Xanthocephalus xanthocephalus*). All three species nest in open meadows and marshes in the Tahoe National Forest, California, where our study was conducted. Brewer's Blackbirds nest in substrates ranging from grasses to trees, typically near flowing water. Red-winged Blackbirds on our study site favor lush grasses over shallow (<1 m) water as nest sites, and Yellow-headed Blackbirds nest in either cattails (*Typha* spp.) or sedges (*Scirpus* spp.) over deeper (> 1 m) water.

Nests of the three species differ in size and composition. Brewer's Blackbird nests are largest (median dry weight = 77 g, $N = 5$), with woody twigs for an outer layer, walls made of grass, and a shallow nest cup lined with fine, dark roots and grasses. Red-winged Blackbird nests are smaller (median = 55 g, $N = 4$), and composed almost exclusively of grasses woven around the supporting substrate. Nest cups are lined with light brown, pliable twigs. Nests of Yellow-headed Blackbirds are about the same size (median = 52.5 g, $N = 8$) and composed primarily of grasses and sedges. Nest cups are the deepest of the three nest types and lined with broad strips of light-colored grass.

Egg coloration also differs. Brewer's Blackbird eggs are darkest, with a tan ground color and black scrawls and brown spots distributed across the egg surface. Red-winged Blackbird eggs are bright, with a blue ground color; the few black scrawls are primarily on the broad end. Eggs of Yellow-headed Blackbirds have a tan to bluish ground color, with brown spots distributed across the egg surface. For a color plate of nests and eggs, see Westmoreland and Kiltie (1996).

Preparation of eggs and nests. Egg reflectivity was quantified with a Colortron[®] reflectance spectrophotometer (Light Source, San Rafael, California). We used 12 eggs from each species, with three reflectance measures taken near the equator of each egg and averaged. For Red-winged Blackbird eggs, we measured only the blue ground color because the dark scrawls are typically confined to the broad end and intercept little incident sunlight. For the other two species, we made no attempt to discriminate ground color from speckling because speckles are distributed across the egg surface and were smaller than the aperture of our spectrophotometer. The spectrophotometer illuminated egg surfaces with simulated sunlight projected

at a 45° angle through a 9-mm² aperture and recorded reflected light in 10 nm bandwidths from 400–700 nm, the waveband at which eggshell pigments have the greatest absorption (Bakken et al. 1978). The spectrophotometer was calibrated against a white standard before use. Reflectivity was calculated as the total area under the reflectance curve.

We used 54 eggs during field trials of heat acquisition. These eggs were selected from 54 clutches collected during previous field seasons, cleared of yolk and albumin, and stored in the dark to prevent fading. The narrow end of each egg was punctured with a pin, and the broad end drilled to create a 9.5-mm² opening. Egg volume was measured by sealing the pinhole and filling eggs with water. Nests used during experiments had been collected in prior field seasons. During experiments, nests were fixed in their natural upright positions by placing them in white plastic gardening pots.

Experimental design and field procedure. Eggs were randomly grouped into 18 triads, with each triad containing three eggs (one of each species). During field trials, pinholes were sealed with soft wax and eggs were filled with refrigerated (20°C) albumen; a Hobo® thermistor (Onset Computer Corporation, Bourne, Massachusetts) was inserted through the broad end of each egg. The temperature-sensitive tip of the thermistor extended about 2/3 of the distance from the broad end of the egg, and recorded core egg temperature ($\pm 0.7^\circ\text{C}$) every min for 70 min. Avian embryos are positioned near the top center of eggs so we did not quantify temperatures at the site of embryogenesis. An additional thermistor was suspended in the nest cup to measure ambient air temperature. We covered thermistor leads with white towels to prevent heat gain from sunlight.

Eighteen nests (six per species) housed the triads during experimental trials. In a crossed experimental design, nine triads and nests were exposed to full sunlight and the other crossed triads and nests were placed under a diffusing umbrella. To estimate the difference in illumination between treatment (exposed) and control (shaded) conditions, Hobo® light intensity meters were positioned in both environments. These loggers recorded illumination from 400–700 nm, expressed in log lumens/m². Treatment and control nests were placed 2 m apart in an open meadow (elevation 2000 m) in the Tahoe National Forest,

California, between 10:00 and 13:00 (Pacific Standard Time) from 5–12 July 1999. During trials, skies were cloudless and sunlight directly illuminated treatment eggs. Relative humidity (15–25%) and wind speed (5–15 knots) varied among trials, but because treatment and control nests were presented simultaneously and all egg phenotypes were present in both, the experimental design controlled for such environmental variation. Although overhead vegetation may partially shade nests under natural conditions, we maximized solar irradiation to enhance detection of egg-color effects.

Curve fitting. To fit a curve to the rise in temperature for each egg, we used the heating equation $T_t = T_\infty + (T_o - T_\infty)e^{-\alpha t}$, where T_t is egg temperature at time t , T_∞ is the asymptotic temperature, T_o is the initial temperature, and t is time. The constant α , when inverted ($1/\alpha$), is a dimensionless “time constant” that represents an object’s rate of response to an abrupt change in environmental temperature (Kreith 1965) such as sudden exposure to solar irradiation. The time constant is equal to $(cpV)/(Ah)$, where c is the specific heat of the egg, p is density, V is volume, A is surface area, and h is the heat transfer coefficient. We could not compare $1/\alpha$ between treatment and control eggs because the two groups did not have equivalent values for T_o and T_∞ . In the field, control triads were filled with albumen prior to treatment triads, so T_o for control eggs averaged $19.3 \pm 3.9^\circ\text{C}$ whereas T_o for treatment triads averaged $25.2 \pm 3.8^\circ\text{C}$. In addition, treatment triads were exposed to full sunlight and reached higher T_∞ than control triads.

Data analysis. Egg reflectivity and egg volume were analyzed using one-way ANOVA with the Scheffe correction for multiple comparisons. To examine effects of treatment, egg phenotype, and nest type on heat acquisition, we analyzed two dependent variables: asymptotic egg temperature (the first temperature to remain stable for 15 consecutive min) and the time required to reach asymptotic temperature (min). Time constants derived from the heating equation were analyzed similarly, except that treatment and control groups were separated prior to analysis. In each case, we first ran a full-model ANCOVA that included egg volume as the covariate and all two-way interaction effects, and followed with a reduced model where the covariate and non-significant interactions were eliminated.

One Yellow-headed Blackbird egg in the treatment group was not used in our heat acquisition analyses because the datalogger failed before recording an asymptotic temperature.

RESULTS

Eggs of the three species differed in volume and reflectivity (Table 1). Brewer's Blackbird eggs had about 10% greater volume than eggs of Red-winged Blackbirds, whereas eggs of the Yellow-headed Blackbird were intermediate in size and not significantly different from the other species. Because volume differences were not controlled experimentally, we statistically removed any effect during analyses of heat acquisition by using egg volume as a covariate in the first set of ANCOVAs. Because egg volume never contributed significantly to any model, it was dropped from the second series of analyses.

Egg reflectivity paralleled human perception (Table 1). Red-winged Blackbird eggs were the most reflective, Yellow-headed Blackbird eggs intermediate, and Brewer's Blackbird eggs darkest. The difference between the eggs of Red-winged and Brewer's blackbirds was nearly two-fold (Table 1).

Light saturation within the visible range differed markedly between treatment and control environments. Light intensity was 66% higher in treatment environments (4.18 ± 0.06 log lumens/m²) than in control environments (3.96 ± 0.03 log lumens/m², $P < 0.01$), and ambient nest-cup temperatures, averaged over the 70-min trials, were significantly higher for nests in direct sunlight (treatment nests, 40.5 ± 0.8 °C; control nests, 31.7 ± 0.9 °C, $P < 0.0001$).

Heat acquisition—egg comparisons.

Time constants of heat acquisition curves did not differ under shaded conditions (Table 2). When eggs were exposed to sunlight, however, the time constant for Brewer's Blackbird eggs was

significantly greater than that for Red-winged Blackbird eggs. Eggs of all three species reached a higher asymptotic egg temperature, and reached asymptotic temperature more quickly, when exposed to full sunlight than when shaded (Table 3).

The critical test of the thermoregulation hypothesis is the treatment-by-egg interaction. If egg reflectance influences heat acquisition from sunlight, differences in color should have their greatest effect when eggs are exposed to direct solar radiation, and such differences should disappear when eggs are shaded. We did not test the interaction effect in analyses of time constants because treatment and control groups were non-comparable (see Methods), but the test could be done for the other dependent variables. In both cases, the treatment-by-egg interaction was not significant ($P = 0.62$ for asymptotic temperature and $P = 0.75$ for time to reach asymptotic temperature) in the full models.

Heat acquisition—nest comparisons.

When placed in the nests of different species, eggs ultimately reached equivalent asymptotic temperatures, but did so at different rates (Table 4). Eggs took significantly longer to reach asymptotic temperature in Yellow-headed Blackbird nests than in Brewer's Blackbird ($P = 0.003$) or Red-winged Blackbird ($P = 0.05$) nests. For all of these comparisons, nest-by-treatment interaction effects were not significant ($P > 0.05$), indicating that differences between species were due to structural properties of nest architecture, not to radiation being absorbed differentially by nest linings.

DISCUSSION

Our results do not support the thermoregulation hypothesis; differently pigmented eggs acquired heat at equivalent rates in both light-saturated and light-diffused environments. In

Table 1. Blackbird eggs differed in volume ($N = 18$) and reflectivity ($N = 12$). Means in the same column with the same superscript are not significantly different ($P < 0.05$; Scheffe post hoc comparisons).

Species	Egg volume (ml) Mean \pm 1 SE	Egg reflectivity ^a Mean \pm 1 SE
Brewer's Blackbird	5.0 ± 0.4^A	0.21 ± 0.02^A
Red-winged Blackbird	4.4 ± 0.6^B	0.40 ± 0.01^B
Yellow-headed Blackbird	4.7 ± 0.4^{AB}	0.28 ± 0.02^C

^a % of total reflectance.

Table 2. Time constants of heat acquisition curves differed in exposed conditions, but not in shaded environments. Within columns, means with the same superscript are not significantly different.

Species	Treatment eggs		Control eggs	
	N	Mean \pm 1 SE	N	Mean \pm 1 SE
Brewer's Blackbird	9	54.5 \pm 11.0 ^A	9	31.6 \pm 3.67 ^A
Red-winged Blackbird	9	26.8 \pm 4.16 ^B	9	28.9 \pm 3.88 ^A
Yellow-headed Blackbird	8	31.1 \pm 8.70 ^{AB}	9	34.6 \pm 5.16 ^A

contrast, Montevecchi (1976) and Bertram and Berger (1981) reported that darker eggs acquired heat significantly faster. One possible explanation for these differences is the species studied—blackbirds in our study versus Laughing Gulls (*Larus atricilla*), domestic hens (*Gallus gallus*), and Ostriches (*Struthio camelus*). We believe this explanation unlikely. Kennedy and Vevers (1976) surveyed the eggshell pigments of 43 families of birds in 18 orders, and found that variation in egg coloration was almost entirely due to differences in deposition of three pigments: protoporphyrin (brown), biliverdin (blue), and zinc biliverdin chelate (green). Because all of these pigments have low absorbance in the near-infrared range of wavelengths, and about one-half of sunlight falls within this range (Bakken et al. 1978), they are unlikely to differentially influence heat gain. The eggs used in our study varied dramatically in the deposition of protoporphyrin and biliverdin, but we observed

no differences in heat gain even when they were placed in a setting that maximized irradiation.

More likely, the difference between our findings and those of previous investigators is due to differences in experimental design. Montevecchi (1976) used white paint to alter the color of Laughing Gull eggs, and khaki paint to alter hen eggs; moreover, he placed eggs on a wooden platform that might have contributed more heat via conduction than a nest. Bertram and Berger (1981) used crayons and dyes to alter Ostrich eggs. Such artificial pigments probably do not effectively mimic the unique reflectance spectra of natural eggshell pigments.

One trend in heat acquisition in our study suggests a possible influence of egg color. In treatment environments, Brewer's Blackbird eggs had a significantly ($P < 0.05$) greater time constant than Red-winged Blackbird eggs (Table 2). This trend was not observed in shaded environments, suggesting that the darker-pigmented Brewer's

Table 3. Eggs of the three species of blackbirds did not differ in asymptotic temperature, or the time required to reach asymptotic temperature. There are no significant ($P < 0.05$) differences within columns.

Variable Species	Treatment eggs		Control eggs		P
	N	Mean \pm 1 SE	N	Mean \pm 1 SE	
Asymptotic egg temperature (°C)					
Brewer's Blackbird	9	45.6 \pm 0.1	9	32.0 \pm 1.3	
Red-winged Blackbird	9	44.2 \pm 0.7	9	31.3 \pm 1.3	
Yellow-headed Blackbird	8	44.5 \pm 0.7	9	32.3 \pm 1.4	
Final model ^a : Treatment effect					< 0.0001
Egg effect					0.62
Time required to reach asymptotic temperature (min)					
Brewer's Blackbird	9	49.7 \pm 10.2	9	81.1 \pm 11.4	
Red-winged Blackbird	9	67.9 \pm 11.7	9	81.8 \pm 10.4	
Yellow-headed Blackbird	8	59.8 \pm 4.5	9	91.0 \pm 13.7	
Final model ^a : Treatment effect					0.003
Egg effect					0.46

^a Interaction effects and egg volume were not significant in the full models, and thus dropped from the final models.

Table 4. Eggs placed in nests of blackbird species did not differ in asymptotic temperature, but did differ in the time required to reach asymptotic temperature.

Variable	Treatment eggs		Control eggs		P
	N	Mean \pm 1 SE	N	Mean \pm 1 SE	
Asymptotic egg temperature ($^{\circ}$ C)					
Brewer's Blackbird	9	44.6 \pm 0.7	9	32.1 \pm 0.9	
Red-winged Blackbird	9	44.9 \pm 0.7	9	30.9 \pm 0.6	
Yellow-headed Blackbird	8	44.8 \pm 0.5	9	32.6 \pm 2.0	
Final model ¹ : Treatment effect					< 0.0001
Nest effect					0.73
Time required to reach asymptotic temperature (min)					
Brewer's Blackbird	9	47.7 \pm 4.2	9	66.2 \pm 3.8	
Red-winged Blackbird	9	51.3 \pm 6.8	9	84.3 \pm 12.7	
Yellow-headed Blackbird	8	80.6 \pm 13.3	9	103.3 \pm 13.2	
Final model ¹ : Treatment effect					0.003
Nest effect ²					0.002

¹ Interaction effects and egg volume were not significant in the full models.

² Eggs in Yellow-headed Blackbird nests took significantly ($P < 0.05$) longer to reach asymptotic temperature. Other comparisons were not significant.

egg experienced a greater rate of heat gain in full sunlight. However, the heating curves in Figure 1 do not support this interpretation. Rather, the anomalous (yet within 1 SD) drop in mean temperature for Brewer's Blackbird eggs in the last 10 min of treatment trials probably explains the higher time constant. The temperature drop induced a more curvilinear trend line

for Brewer's Blackbird eggs, and thus a higher time constant was derived. In essence, we believe that this was a case of Type I error.

To what extent can our findings be generalized to other species? We studied three blackbird species whose eggs differ significantly in reflectance (Table 1), and exposed clutches to greater irradiation than they would

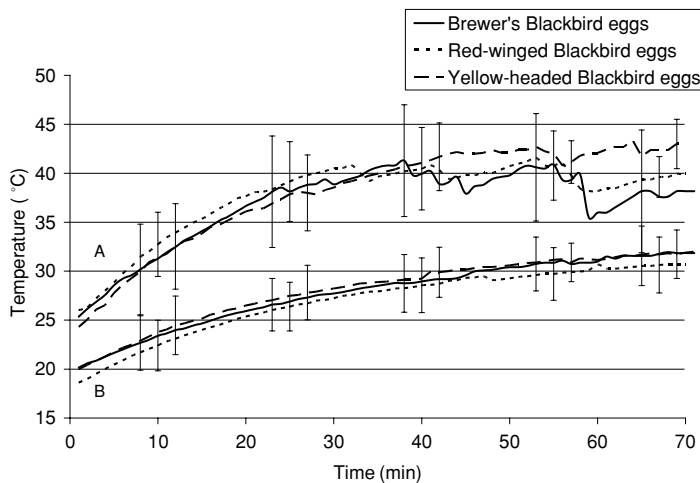


Fig. 1. Heat acquisition was unrelated to egg color in three blackbird species. A, eggs exposed to direct sunlight. B, eggs shaded by a diffusing umbrella. Vertical bars represent \pm 1 SD from the mean. For each group of three error bars, the first represents Brewer's Blackbird eggs, the second Red-winged Blackbird eggs, and the third Yellow-headed Blackbird eggs.

encounter under natural conditions. We believe our findings are relevant to most passerine species nesting in partially shaded habitats with moderate environmental temperatures. In hot, unshaded nesting environments, such as coastal plains used by shorebirds, for example, Laughing Gulls (Montevocchi 1976), Heerman's Gulls (*Larus heermanni*; Bennett and Dawson 1979), Black-necked Stilts (*Himantopus mexicanus*; Grant 1982) or platform nests placed in treetops by herons, differences in solar absorption by eggshell pigments could be physiologically significant. The three major pigments are uniform in reflecting the near-infrared wavelengths, but differ substantially in the 320–700 nm waveband. Blue pigments have higher overall reflectance (Bakken et al. 1978), and thus provide a potential thermoregulatory advantage. However, shorebirds typically have eggs with beige to brown ground colors and darker speckling (Baicich and Harrison 1997). This indicates either that the thermoregulatory influence of lighter pigments is insignificant, or that selection for crypsis is stronger than selection for thermoregulation. Herons have light blue to olive eggs without speckling; perhaps selection for thermoregulation is stronger in treetop nests that are inaccessible to ground predators. As Bakken et al. (1978) noted, however, it is unclear why these eggs should be pigmented at all. The underlying white color of avian eggshells provides 70–95% reflectance.

Nest architecture is known to influence the thermal environment of eggs (White and Kenney 1974, Kern and van Riper 1984), and intraspecific variation in nest architecture is related to latitude (Kern 1984). Among the species we studied, the nests of Yellow-headed Blackbirds appeared to be the least well insulated. Egg triads within these nests took the longest to reach asymptotic temperature, indicating that the retention of heat from incident sunlight was lower (Table 4). Because the nest-by-treatment interaction was not significant for either of these indices, nest coloration (light in the Yellow-headed Blackbird, darker in the other species) cannot explain the difference. Nest mass is known to correlate with insulation value (Hoi et al. 1994), but in this case, differences in nest mass do not parallel the trend observed in Table 4 because Yellow-headed Blackbird nests are about the same size as those of Red-winged

Blackbirds. We hypothesize that the difference in heat retention is due to different nest-bowl linings. Brewer's and Red-winged blackbirds line nest cups with vegetation of fine diameter. In contrast, Yellow-headed Blackbird nests are lined with coarse vegetation that may leave openings for air flow; nest porosity increases thermal conductance (Kern 1984), and the absence of a nest lining of fine material can increase the rate of heat loss by more than 35% (Kern and van Riper 1984). Because our experiments involved nests removed from their natural substrates, we cannot conclusively say whether nests of these species would differ in heating rates in their natural environments. It would be interesting to translocate clutches between nests in their original substrates to determine if differences in the thermal environment exist, and if they influence embryo survival.

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