



Egg coloration and selection for crypsis in open-nesting blackbirds

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High variation in egg coloration among birds has traditionally been explained as adaptation for camouflage. We tested this hypothesis by conducting reciprocal clutch exchanges ($n = 301$) among Brewer's blackbirds *Euphagus cyanocephalus*, red-winged blackbirds *Agelaius phoeniceus*, and yellow-headed blackbirds *Xanthocephalus xanthocephalus*. We predicted that clutches placed against their natural nest backgrounds would have higher survival rates than heterospecific clutches. Intraspecific clutch exchanges were used as a control. Clutch survival was monitored for a 9-d period at all nests, during which time incubation rhythm and nest defense were quantified. Intraspecific clutch exchanges did not influence incubation or nest defense. For two of the species, intraspecific clutch exchanges did not influence clutch survival; in red-winged blackbirds, however, intraspecifically exchanged clutches had somewhat depressed survival curves relative to control clutches ($P = 0.08$). The effect of interspecific clutch exchanges differed by host species. In Brewer's nests, eggs of the yellow-headed blackbird had lower survival than Brewer's eggs ($P = 0.02$), but survival of red-winged blackbird eggs did not differ from Brewer's eggs ($P = 0.50$). In nests of red-winged blackbirds, all three clutch types had approximately equal survival. In yellow-headed blackbird nests, eggs of the red-winged blackbird had lower survival than yellow-headed blackbird eggs ($P = 0.06$), and survival of Brewer's eggs did not differ from yellow-headed blackbird eggs ($P = 0.31$). These findings support a role for egg coloration as camouflage in two of the three species studied.

Avian eggs have remarkable interspecific variation in coloration, ranging in hue from light blue to reddish-orange, in brightness from white to nearly black, and in pattern from spotless to heavily spotted (Harrison 1978, Kilner 2006). Biologists have attributed this high phenotypic diversity to several selection pressures (recently reviewed in Kilner 2006). For species that leave clutches exposed to direct sunlight, coloration may modulate egg temperature (Bertram and Burger 1981, Montevecchi 1976; but see Bakken et al. 1978, Westmoreland et al. 2007). In species that suffer frequent nest parasitism, selection favors egg colors that diverge from the parasite's egg phenotype. Species that lay blue-green eggs may use egg color as a post-mating signal of female quality (Moreno et al. 2005, 2006).

Because these hypotheses apply to species with specific nesting characteristics, they leave much of the

variation in egg coloration unexplained. Many birds nest in shaded habitats, or have incubation rhythms that expose the eggs to sunlight only for short periods (Kendeigh 1952, Skutch 1976), in addition, many species are egg acceptors (sensu Rothstein 1982), showing no response to the eggs of nest parasites. The pigment which is responsible for blue-green coloring is absent in about half of bird species (Kennedy and Vevers 1976). Thus the traditional explanation for interspecific variation in egg color, camouflage (Wallace 1890, Cott 1940, von Haartman 1957, Harrison 1968), may apply to a broad spectrum of avian species. The value of egg coloration as camouflage, however, has been called into question because many experiments testing this hypothesis have failed to find differences in survival rates among eggs that differ in color or pattern (Underwood and Sealy 2002). On the other hand, most

of these experiments employed artificial nests or eggs, so their relevance to natural nests is unclear.

We tested the camouflage hypothesis in three species of blackbirds (Icteridae) that do not respond to nest parasitism, yet have distinctly different egg phenotypes (see Westmoreland and Kiltie 1996 for a color print)-the Brewer's blackbird *Euphagus cyanocephalus*, the red-winged blackbird *Agelaius phoeniceus*, and the yellow-headed blackbird *Xanthocephalus xanthocephalus*. Our preliminary experiments with eggs of these species indicate no thermoregulatory influence (Westmoreland et al. 2007). In a previous study (Westmoreland and Kiltie 1996), we assessed the quality of camouflage using three metrics based on brightness variation and found that, for two camouflage metrics, the species differed significantly. Surprisingly, we failed to detect a positive relationship between the quality of camouflage and clutch survival. For the red-winged blackbird, in fact, we found that less cryptic clutches had higher survival rates.

Our previous examinations of camouflage and survival were done within species. In this study, we increased the magnitude of color variation by transplanting clutches among species. The camouflage hypothesis predicts that, if egg phenotypes differ in survival, clutches composed of the same phenotype placed against the natural (conspecific) nest backgrounds will have higher survival rates than hetero-specific clutches.

Materials and methods

Study sites and reproductive biology of the study species

The three species are common nesters in the Tahoe National Forest of California USA. Three study sites were used during the May-June nesting seasons of 1990–1993. The first (39° 30'N, 120° 19'W) is a natural meadow within the national forest approximately 5 km east of Webber Lake, where Brewer's and red-winged blackbirds nest in grasses and willow shrubs *Salix* spp. on the periphery of oxbow ponds. The second site (38° 00'N, 120° 20'W), near Sierraville California, is an ancient lake bed that is now devoted to cattle ranching. All three species nest at high densities in native vegetation along roadsides and in fields. At this site, we avoided locations that were clearly modified by ranching. At the third site, near Loyalton California, a natural spring (42°30'N, 120°20'W) sustains a large cattail *Typha* spp. and sedge *Scirpus* spp. marsh where yellow-headed blackbirds nest in high densities, and red-winged blackbirds nest along the marsh edges.

The three species overlap in nesting habitat and breeding season. Brewer's blackbirds are generalists, nesting in trees, shrubs, and grasses. Nests used in this

study were built near running water and located in shrubs or grasses. Brewer's nests are lined with dark twigs of small diameter (0.1–0.4 mm), and where available, horsehair. This creates a background that is darker and finer-grained than that of the other species. The modal clutch size for Brewer's clutches is five eggs. Yellow-headed blackbirds weave their nests into cattails and sedges over standing water. The nest is lined with strips of broad vegetation (6–10 mm diameter) that become yellow with age. Modal clutch size is three eggs. Red-winged blackbirds typically nest in grasses over shallow water. Their nests are lined with light-colored, pliable twigs and rootlets of intermediate diameter (0.5–1.4 mm). They typically lay four eggs per clutch. The mean \pm se julian dates of nest initiation during the four-year study period were: Brewer's blackbirds, 150 ± 1 d ($n = 69$); red-winged blackbirds, 156 ± 0.8 d ($n = 80$); and yellow-headed blackbirds, 156 ± 0.7 d ($n = 64$). Incubation periods among the species range from 10–12 d.

The species differ substantially in egg coloration (for a colour plate, see Westmoreland and Kiltie 1996). Red-winged blackbird eggs have a blue ground color with a few black scrawls that are distributed mainly on the broad end. Yellow-headed blackbirds lay eggs with a tan to bluish ground color, and brown speckles spread across the entire egg. Brewer's blackbird eggs are darkest; they have a tan ground colour with black speckles and scrawls distributed over the egg surface. Within the 400–700 nm range of wavelengths, red-winged blackbird eggs have twice the reflectivity of Brewer's eggs, and yellow-headed blackbird eggs are intermediate between the other species (Westmoreland et al. 2007). Brewer's blackbird eggs are about 15% larger by volume (ml) than red-winged blackbird eggs; other comparisons among species are nonsignificant (Westmoreland et al. 2007).

Where habitats are mosaic, nests of the three species can be found in close proximity. In our study areas, nests of Brewer's blackbirds and red-winged blackbirds are often found within a few m of each other; red-winged blackbird nests are also found on the periphery of marshes dominated by yellow-headed blackbirds. Despite the proximity, differences in nest accessibility probably result in exposure to different predators. Predators that have been observed at nests include a California ground squirrel *Citellus beecheyi* at a Brewer's nest, several mountain garter snakes *Thamnophis elegans elegans* at red-winged nests, and a sedge wren *Cistothorus platensis* at a yellow-headed nest. The deep water (often 1 m or greater) under yellow-headed blackbird nests may preclude predation by small mammals and reduce predation pressure from snakes.

Identification of nest predators is a persistent problem in avian biology (Picman 1987). Researchers generally assume reptilian or avian predation when the

nest architecture is undisturbed and there are few or no eggshells remains. Predation by small mammals is indicated by an intact nest containing empty eggshells, and predation by larger mammals is assumed when the nest is destroyed. By these criteria, >95% of the predation events on our study sites could be attributed to reptilian and avian species.

Field procedure

Nests were discovered by observing females as they departed from or returned to their nests, and by searching appropriate habitat. Ninety-three Brewer's nests, 109 red-winged nests, and 99 yellow-headed nests were used in experiments. Each nest was randomly assigned to one of four treatments with the following probabilities: (1) control, 1/6, (2) intraspecific clutch exchange, 1/6, (3) interspecific clutch exchange with one species, 1/3, and (4) interspecific exchange with the remaining species, 1/3. In many cases, treatments could be established immediately; in others, treatments were established 1–3 d later, when the appropriate foster clutch became available. Most clutches (96%) contained four eggs. With two exceptions, a single egg was removed from control clutches of Brewer's blackbirds (modal clutch size of 5 eggs). For red-winged (modal clutch of 4 eggs) and yellow-headed (modal clutch of 3 eggs) blackbirds, clutches containing less than 4 eggs were usually passed over when assigned as controls. There were a few exceptions: 2 red-winged, and 2 yellow-headed control clutches had 3 eggs each.

The day that treatments were established was labeled day 0; thereafter, clutches were checked on days 3, 6, and 9. We minimized time spent at the nest because researcher disturbance is known to influence predation frequency for some species (Westmoreland and Best 1985). To avoid leaving scent trails, we used a fiberglass pole from a distance of 3 m to position a mirror over the nest. If eggs were present, the observer left within 90 s. Adults were often absent during nest checks; when an adult was present and defended the clutch, the observer remained 3 m from the nest for 2 min to record defensive behavior, which in red-winged blackbirds is related to clutch survival (Weatherhead 1990). Brewer's and red-winged blackbirds typically defend eggs, but yellow-headed blackbirds do not. Nest defense was quantified as the number of vocalizations and the closest approach to the observer made by the defending adult. The 2 min observation was never repeated at a nest. Nest defense intensifies as offspring mature in some species (Biermann and Robertson 1981, Regelman and Curio 1983, but see Knight and Temple 1986, Westmoreland 1989), potentially biasing our comparisons of nest defense among treatments. To detect this possible bias we determined the "pertinent

age" of clutches (i.e., the number of days that adults had been attending a nest with eggs) by observing the hatching date of a breeding pair's original clutch, and backdating. This was only possible when at least one egg of the original clutch, which was being used in another treatment, survived to hatch.

For nests that could be viewed from a distance of at least 50 m (41 Brewer's, 40 red-winged, 41 yellow-headed), we quantified the female's incubation rhythm. Observations originally lasted 2 h, but were shortened after we learned that females take frequent breaks at consistent intervals. Timed observation began when a female arrived at the nest; for the next 30 min we recorded the total time spent away from the nest (min) and the number of incubation bouts.

Statistical analysis

Variables used to quantify nest defense and incubation rhythm were analyzed with Mann-Whitney U-tests or Kruskal-Wallis tests. To quantify clutch survival we counted the number of days that a clutch remained undamaged by predators. We considered full clutch loss and partial clutch loss to be equivalent failures of camouflage because eggs had been discovered. Partial clutch loss occurred in 59 of the 129 (46%) predation events we observed. Clutch survival was analyzed by Fisher exact tests via the SAS/STAT FREQ procedure, and by estimation of nonparametric Kaplan-Meier survival distribution functions via the SAS/STAT Lifetest procedure (SAS 2006). The Fisher test compares binary frequencies (success or failure) among categories (host nests). The Lifetest procedure calculates the survival distributions of specified groups, then applies nonparametric methods to discriminate differences in their survival curves. In determining P values, we used log-rank statistics, which emphasize longer-term survival differences (in this case, toward the end of the 9-d observation period) as opposed to early survival differences. This was more appropriate to our determination of whether eggs would differ in the probability of survival to hatching.

Because a directional prediction was implied by the pairwise hypotheses under test, we calculated 1-sided P values. For tests on intraspecific transplantation, the alternative hypothesis was that transplanted clutches failed relatively more often than nontransplanted clutches (Fisher tests) or that the survival function for transplanted clutches was significantly depressed in comparison to those not transplanted (Lifetest procedure). For tests on interspecific transplantation, the alternative hypothesis was that interspecific transplants failed relatively more often than intraspecific transplants and those not transplanted at all (Fisher tests) or that the survival function for interspecifically transplanted

clutches was significantly depressed in comparison to intraspecific transplants and those not transplanted at all (Lifetest procedure). A one-sided Fisher test assumes that row and column totals are fixed and uses the hypergeometric distribution to compute the probability of obtaining tables with frequencies greater than or equal to that of the cell in row 1, column 1 of the observed table (Agresti 2002). A small P-value supports the alternative hypothesis that the probability of the first cell, whose frequency completely determines the 2×2 table when the marginal row and column sums are fixed, is greater than that expected under the null hypothesis (SAS 2006). One-sided tests for the Lifetest procedure were obtained from this procedure's Trend option available in SAS version 9.1, with a correction for the fact that two-sided $Pr > |z|$ -values are mistakenly output from the trend tests (P.T. Savarese, SAS, pers. comm.). For pairwise comparisons in which a clear prediction was possible (e.g., heterospecific clutches should have lower survival than conspecific clutches in a species' nest), we calculated 1-tailed P values.

Results

Survival of host nests

Disregarding clutch phenotype, host nests differed in survival. Yellow-headed blackbird nests had the highest survival, Brewer's nests were intermediate, and red-winged blackbird nests had lowest survival (Fig. 1). Differences were significant only between yellowheaded and red-winged blackbird nests ($P = 0.002$).

Intraspecific clutch exchanges

Exchange of clutches had no apparent influence on adult behavior. Adults with foster clutches did not differ

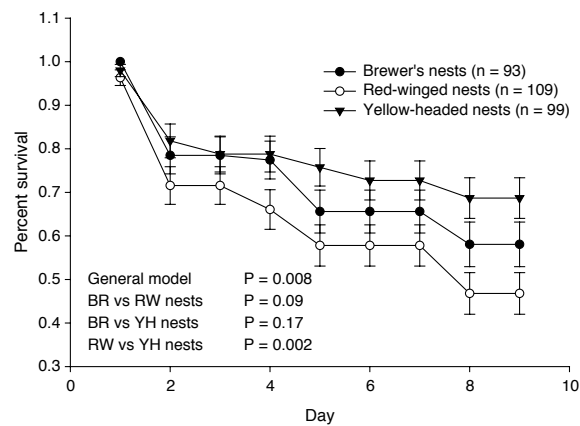


Fig. 1. Comparisons of clutch survival in nests of the three blackbird species. Vertical bars are SE.

significantly from adults with control clutches in nest defense (vocalizations per min: Brewer's blackbird $P = 0.27$, red-winged blackbird $P = 0.20$; closest approach to investigator: Brewer's blackbird $P = 0.29$, red-winged blackbird $P = 0.45$), or incubation rhythm (clutch exposure: Brewer's blackbird $P = 0.59$, red-winged blackbird $P = 0.46$, yellow-headed blackbird $P = 0.82$; bouts of incubation per 30 min: Brewer's blackbird $P = 0.63$, red-winged blackbird $P = 0.97$, yellow-headed blackbird $P = 0.60$). Our indices of nest defense did not appear to be biased by the pertinent ages of original vs foster clutches, but sample sizes were low. For Brewer's blackbirds, median relevant ages on the day that nest defense was quantified were: original clutches ($n = 5$), 6 days; foster clutches ($n = 2$), 12.5 days, $P = 0.33$, Mann-Whitney U-test. For red-winged blackbirds, the values were: original clutches ($n = 6$), 6 days; foster clutches ($n = 3$), 8 days; $P = 0.34$. Yellow-headed blackbirds do not defend nests during the incubation stage.

For Brewer's and yellow-headed blackbird nests, intraspecifically exchanged clutches did not differ from control clutches in survival (Table 1, Fig. 2). For these species, we pooled exchanged and nonexchanged clutches into a single control group when analyzing the effects of interspecific clutch exchanges. In red-winged blackbird nests, the effect of intraspecific clutch exchange was ambiguous. While the two clutch types did not differ in the frequencies of survival or failure (Table 1, $P = 0.21$), Lifetest analysis suggested a depressed survival curve for exchanged clutches relative to control clutches (Fig. 2, $P = 0.08$). To be conservative in testing the camouflage hypothesis for this species, we did not pool the two groups as a single control when analyzing interspecific exchanges, but instead used exchanged clutches alone as the control group.

Table 1. Survival of intraspecifically exchanged clutches and eggs during the 9-d observation period. One-tailed P-values were determined from Fisher's exact tests.

	Clutch survival			
	n	Survived	Failed	Percent survival
Brewer's blackbird				
Original clutch	15	10	5	66.7%
Foster clutch	16	10	6	62.5%
P		$P = 0.55$		
Red-winged blackbird				
Original clutch	19	12	7	63.2%
Foster clutch	18	8	10	44.4%
P		$P = .21$		
Yellow-headed blackbird				
Original clutch	15	10	5	66.7%
Foster clutch	17	13	4	76.5%
P		$P = 0.84$		

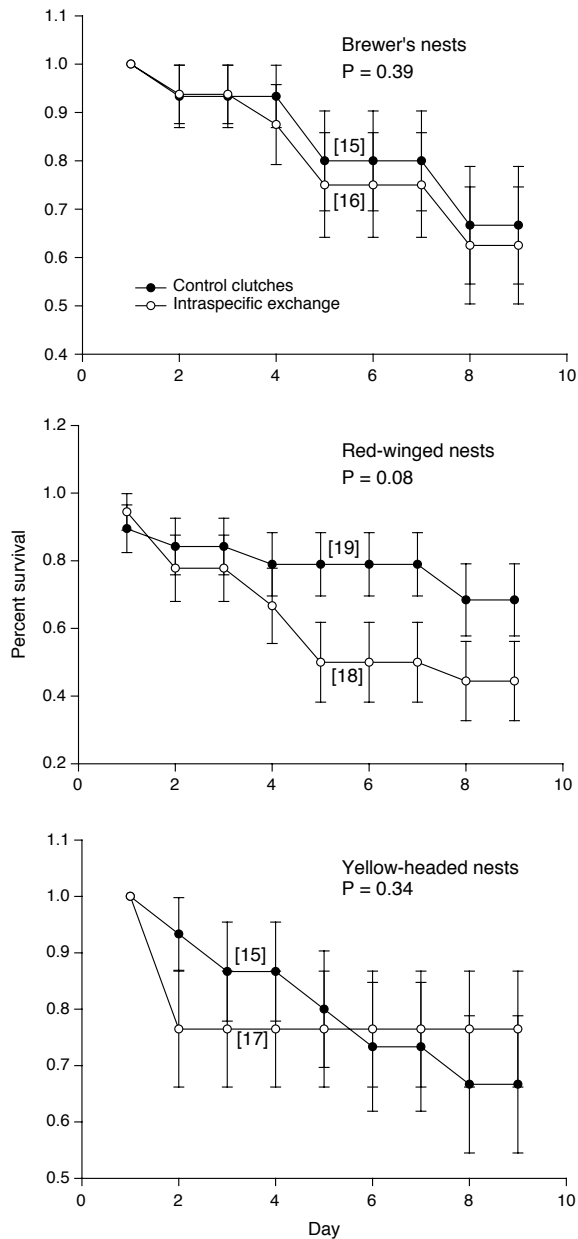


Fig. 2. Comparisons of clutch survival between control and intraspecific clutch exchanges. P-values are based on 1-tailed analyses predicting depressed survival curves for transplanted clutches. Vertical bars are SE, and sample sizes are in brackets.

Interspecific clutch exchanges

All three species readily accepted foster clutches. There were no significant differences among control and treatment clutches in nest defense (vocalizations per min: Brewer's blackbird $P = 0.11$, red-winged blackbird $P = 0.38$; closest approach to investigator: Brewer's

blackbird $P = 0.63$, red-winged blackbird $P = 0.57$) or incubation rhythm (clutch exposure: Brewer's blackbird $P = 0.38$, red-winged blackbird $P = 0.85$, yellow-headed blackbird $P = 0.55$; bouts of incubation per 30 min: Brewer's blackbird $P = 0.96$, red-winged blackbird $P = 0.91$, yellow-headed blackbird $P = 0.59$). As with intraspecific exchanges, treatments did not differ in pertinent clutch age (Brewer's blackbirds, $P = 0.34$; red-winged blackbirds, $P = .58$).

In Brewer's nests, Brewer's and red-winged blackbird clutches had almost equal survival, but Brewer's clutches had higher survival than yellow-headed blackbird clutches (Table 2, Fig. 3). Within red-winged blackbird nests, clutches of the three species did not differ in survival (Table 2, Fig. 3).

When clutches were placed in yellow-headed blackbird nests, there was no difference between survival of Brewer's and yellow-headed clutches; red-winged blackbird clutches had lower survival than yellow-headed clutches. This trend was nearly significant by Fisher exact tests ($P = 0.09$, Table 2) and Lifetest analyses ($P = 0.06$, Fig. 3).

Discussion

Researchers of animal coloration have noted the perplexing nature of egg pigmentation in open-nesting birds (i.e., birds whose nests are not in cavities or enclosed by a dome). One of the founders of the theory of natural selection wrote "the colours of birds' eggs have long been a difficulty on the theory of adaptive

Table 2. Survival of clutches and eggs during the 9-d observation period. One-tailed P-values were determined from 1-tailed Fisher exact tests.

	Clutch Survival			
	n	Survived	Failed	Percent survival
Brewer's blackbird				
Brewer's eggs	31	20	11	64.5%
Red-winged eggs	31	21	10	67.7%
Yellow-headed eggs	31	13	18	41.9%
B vs RW		P = 0.70		
B vs YH		P = 0.06		
Red-winged blackbird				
Brewer's eggs	37	17	20	45.9%
Red-winged eggs	37	20	17	54.1%
Yellow-headed eggs	35	13	22	37.1%
RW vs B		P = 0.32		
RW vs YH		P = 0.11		
Yellow-headed blackbird				
Brewer's eggs	40	31	9	77.5%
Red-winged eggs	27	14	13	51.9%
Yellow-headed eggs	32	23	9	71.9%
YH vs B		P = 0.79		
YH vs RW		P = 0.09		

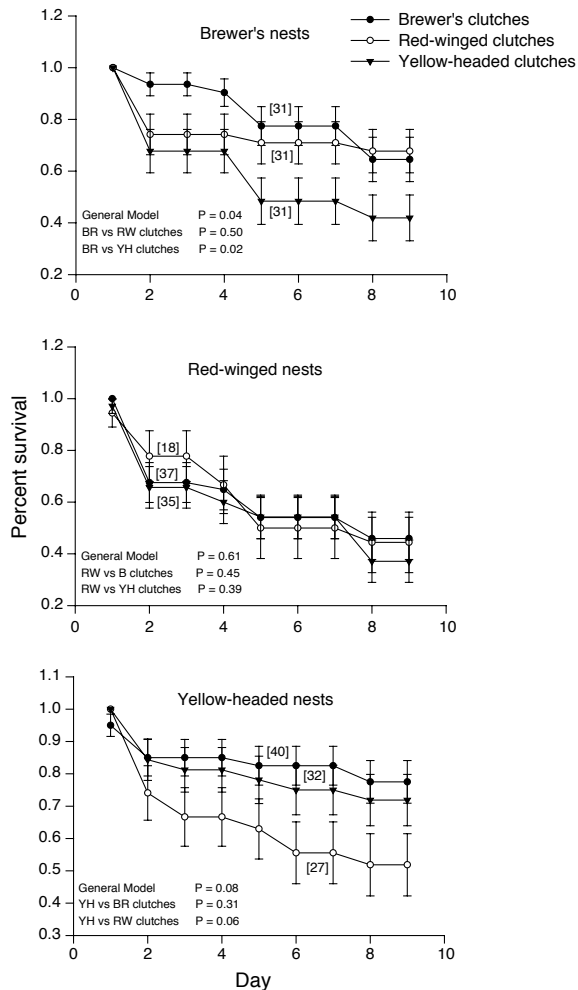


Fig. 3. Interspecific comparisons of clutch survival in nests of three blackbird species. Vertical bars are SE, and sample sizes are in brackets.

coloration, because, in so many cases it has not been easy to see what can be the use of the particular colours, which are often so bright and conspicuous that they seem intended to attract attention rather than to be concealed" (Wallace 1890). Wallace went on to argue that bird eggs are well camouflaged when viewed from below via light penetrating the nest, an assertion that Cott (1940) found "... not at all convincing, and ... quite unsupported by evidence." As recently as 1976, Skutch vigorously argued that egg coloration in most open-nesting species is too conspicuous to be explained as camouflage, and that the target of selection for camouflage is the nest, not the eggs. Götmark's (1993) interspecific comparison of egg color and nest architecture among 27 nonpasserine families supported this view. He found that families constructing conspicuous nests tend to have noncryptic eggs, whereas families

typified by small nests or nest scrapes have less conspicuous eggs. In their review of the adaptive significance of egg coloration, Underwood and Sealy (2002) concluded that egg camouflage "... seems to be adaptive only for species that do not build a nest." The findings reported here, using real eggs and nests constructed in nest sites selected by the birds and actively attended by adults, shows that egg coloration has a significant effect on survival in some species. Most other tests of the camouflage hypothesis have employed artificial nests, artificial egg pigments, or both, and have largely failed to find an effect of camouflage (Underwood and Sealy 2002).

Intraspecific exchanges

In a previous study (Westmoreland and Kiltie 1996), we found that intraspecific variation in clutch camouflage was not related to clutch survival in the Brewer's blackbird and yellow-headed blackbird, and that in the red-winged blackbird, less cryptic clutches actually had higher survival. The current study is to some degree consistent with these findings. Intraspecific exchanges had no effect on clutch survival in Brewer's and yellow-headed blackbirds, but may have had an influence in red-winged blackbird nests. Whether such an effect occurred is equivocal because a Fisher exact test indicates no survival difference between exchanged and unexchanged clutches in red-winged blackbird nests ($P = 0.21$, Table 1), whereas a Lifetest analysis yields a nearly significant difference ($P = 0.08$, Fig. 2), with exchanged clutches having lower survival curves. It is noteworthy that adult red-winged blackbirds did not discriminate between clutches in terms of nest defense or care during incubation.

Interspecific exchanges

We predicted that if clutch phenotypes differed in survival, clutches placed against their natural (conspecific) nest backgrounds would have higher survival than heterospecific clutches. This prediction was clearly supported in Brewer's blackbird nests, where Brewer's clutches had significantly higher survival than yellow-headed clutches (Fig. 3). In yellow-headed blackbird nests, the prediction was also supported. Lifetest analyses indicated that yellow-headed and Brewer's clutches had approximately equal survival, and red-winged clutches were more readily discovered by predators.

The results obtained for red-winged blackbird nests stand in marked contrast to the other species. Against the red-winged nest background, survival differences among clutch phenotypes were far short of statistical significance (Table 2, Fig. 3). This result cannot be

explained by relaxed selection for predator avoidance, because predation on red-winged blackbird nests was significantly higher than predation on the other species' nests (Fig. 2). The question of why an apparently conspicuous egg phenotype does not suffer greater predation is unanswered-unless the fault lies in human inability to effectively assess background matching (Cherry and Bennet 2001)-but this result is not unique to red-winged blackbirds. Götmark (1992) showed that in the song thrush *Turdus philomelos*, a species with blue eggs, pigmentation is largely irrelevant to clutch survival. In the crow tit *Paradoxornis webbiana*, a species in which both blue and white eggs are laid, clutch color is unrelated to nest predation (Kim et al. 1995).

These results suggest that the blue egg coloration of the red-winged blackbird is a neutral trait, or has evolved for some purpose other than camouflage. In the pied flycatcher *Ficedula hypoleuca*, blue egg coloration correlates with the strength of nestling and female immune responses, and apparently induces greater provisioning by the male (Moreno et al. 2005, 2006). The deposition of biliverdin, the egg pigment that imparts blue and green color to eggshells (Kennedy and Vevers 1976) and is an antioxidant, seems to be a postmating signal of female quality. This selective pressure may be applicable to many species, especially for those in which egg coloration is unrelated to predator avoidance.

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