A Blackmail Hypothesis for the Evolution of Conspicuous Egg Coloration in Birds

Authors: Hanley, Daniel, Doucet, Stéphanie M., and Dearborn, Donald C.

Source: The Auk, 127(2) : 453-459

Published By: American Ornithological Society

URL: https://doi.org/10.1525/auk.2009.09090

Commentary

The Auk 127(2):453–459, 2010
© The American Ornithologists' Union, 2010.
Printed in USA.

A BLACKMAIL HYPOTHESIS FOR THE EVOLUTION OF CONSPICUOUS EGG COLORATION IN BIRDS

Daniel Hanley,[1,2,3] Stéphanie M. Doucet,[2] and Donald C. Dearborn[1]

[1]*Department of Biology and Program in Animal Behavior, Bucknell University, Moore Avenue, Lewisburg, Pennsylvania 17837, USA; and*
[2]*Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, Ontario N9B 3P4, Canada*

Naturalists and Evolutionary biologists have long been intrigued by traits that are seemingly maladaptive (Gould and Lewontin 1979, Zahavi and Zahavi 1997, Krüger et al. 2001). The brightly colored eggs laid by many species of birds provide a particularly striking example of such a trait (Wallace 1889, Lack 1958, Lancaster 1964, Underwood and Sealy 2002, Moreno and Osorno 2003, Kilner 2006).

Conspicuous eggs are thought to be costly because they can attract the attention of nest predators and brood parasites (Lancaster 1964, Montevecchi 1976, Götmark 1992, Yahner and Mahan 1996, Castilla et al. 2007, Magige et al. 2008, Westmoreland 2008). As with all visual signals, conspicuousness is not an absolute trait of the egg but depends on the reflectance characteristics of the egg and nesting background, the ambient light in which the egg is perceived, and the visual sensitivity of the signal receiver (Endler 1990). Thus, when referring to conspicuous eggs, we mean eggs that do not match their nesting background in either coloration or pattern. Such eggs could range in color from immaculate blue-green to white, to pink, as opposed to brown or heavily speckled eggs that should be relatively cryptic to visually orienting enemies (Bertram and Burger 1981, Castilla et al. 2007).

Although avian eggs exhibit a great diversity of colors and patterns (Fig. 1), conspicuous eggs are taxonomically widespread, ranging from tinamous (Tinamiformes) to ibises (Ciconiiformes), poorwills (Caprimulgiformes), doves (Columbiformes), and thrushes (Passeriformes) (Cabot 1992, Baicich and Harrison 1997). Here, we develop an alternative to previous hypotheses for the evolution of conspicuous eggs: the blackmail hypothesis proposes that conspicuous egg coloration coerces males into providing additional parental care to offset the increased risk of nest predation or brood parasitism.

Previous Hypotheses for Conspicuous Egg Color

Early hypotheses for the taxonomically broad occurrence of conspicuous eggs included aposematism (Swynnerton 1916, Cott 1948), thermal regulation (Mcaldowie 1886, Bakken et al. 1978), increased visibility in cavities (von Haartman 1957, Holyoak 1969), and camouflage in the greenish light transmitted and scattered by vegetation (Lack 1958). Despite much work on the subject, the evolutionary explanation for conspicuous eggs remains unclear (Underwood and Sealy 2002, Kilner 2006).

A more recent hypothesis concentrates on blue-green eggshell coloration specifically, rather than conspicuousness in a broader sense. This sexual-signaling hypothesis has garnered the most research attention in recent years (e.g., Moreno et al. 2006a, b; Hanley et al. 2008; Soler et al. 2008; Hanley and Doucet 2009). It proposes (1) that blue-green egg pigmentation acts as a signal of female quality (Moreno and Osorno 2003) and (2) that males base investment decisions on this trait. Several studies have found that within species that lay blue-green eggs, males provide more parental care at nests with more chromatic eggs (Moreno et al. 2004, 2006b; Hanley et al. 2008; Soler et al. 2008), and there is some indication that higher-quality females lay eggs that are more intensely blue-green (Moreno et al. 2005, 2006a; Siefferman et al. 2006; Hanley et al. 2008). However, support for the sexual-signaling hypothesis is not universal (Krist and Grim 2007, López-Rull et al. 2007, Hanley and Doucet 2009), and the plausibility of a signaling function, especially in cavity-nesting species, has been questioned (Reynolds et al. 2009). In fact, any universal explanation seems unlikely, given that many of the proposed hypotheses are nonexclusive, and their relevance will probably depend on a species' natural history.

Conspicuous Eggs as Blackmail

As an additional hypothesis, we propose that conspicuous egg coloration may force males to provide additional parental care to offset the increased risk of nest predation or brood parasitism. This hypothesis can explain multiple forms of conspicuous egg

---

[3]E-mail: hanleyd@uwindsor.ca

The Auk, Vol. 127, Number 2, pages 453–459. ISSN 0004-8038, electronic ISSN 1938-4254. © 2010 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/auk.2009.09090

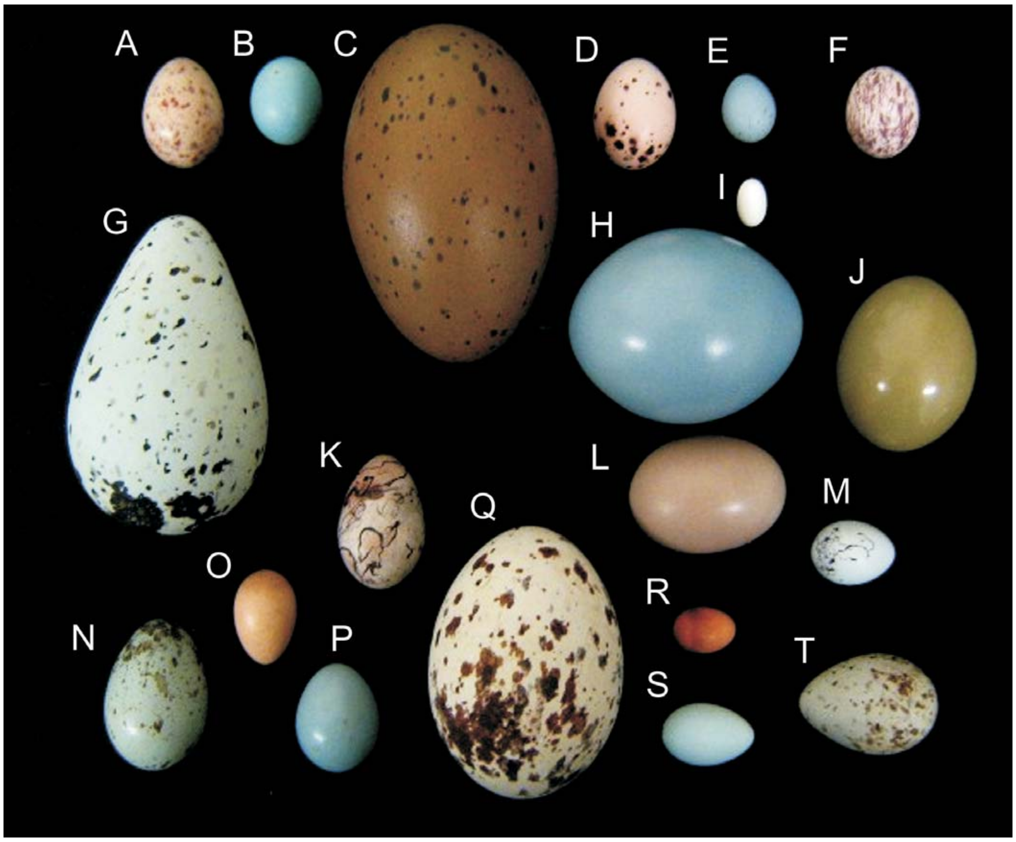

FIG. 1. Birds exhibit extensive variation in the coloration and patterning of their eggs. Here are photographic examples of 20 species that illustrate some of this variation. Voucher numbers from the University of Michigan Museum of Zoology (UMMZ): (A) *Cyanocorax yucatanicus*, UMMZ 191441; (B) *Cuculus solitarius*, UMMZ 238514; (C) *Gavia immer*, UMMZ 34030; (D) *Oriolus chinensis*, UMMZ 191880; (E) *Spizella arborea*, UMMZ 191836; (F) *Myiarchus tyrannulus*, UMMZ 191355; (G) *Uria lomvia*, UMMZ 191176; (H) *Tinamus major*, UMMZ 191600; (I) *Cynanthus latirostris*, UMMZ 198641; (J) *Eudromia elegans*, UMMZ 233501; (K) *Quiscalus major*, UMMZ 191738; (L) *Crypturellus soui*, UMMZ 233500; (M) *Agelaius phoeniceus*, UMMZ 198690; (N) *Corvus brachyrhynchos*, UMMZ 198417; (O) *Campylorhynchus brunneicapillus*, UMMZ 191487; (P) *Aphelocoma ultramarina*, UMMZ 198736; (Q) *Cathartes aura*, UMMZ 238578; (R) *Myiobius atricaudus*, UMMZ 191387; (S) *Ploceus cucullatus*, UMMZ 237206; and (T) *Calidris maritima*, UMMZ 231836.

coloration and might even explain unusual nesting strategies (see below). In the sections below, we describe the blackmail hypothesis, generate a set of testable predictions, and provide several examples that appear to be consistent with this hypothesis.

We propose that sexual conflict load (Houston et al. 2005) may be imposed on males if females produce brightly colored, immaculate eggs in open nests. Highly conspicuous eggs create an increased risk of detection by nest predators or brood parasites (Montevecchi 1976, Castilla et al. 2007, Muñoz et al. 2007) that potentially forces males into providing additional parental care to keep the conspicuous eggs hidden from view. This form of blackmail is similar to the predation risk imposed by nestlings that beg loudly (Zahavi and Zahavi 1997); however, in this situation, conflict arises between the sexes rather than between parents and offspring. Conflict between the sexes occurs because the evolutionarily optimal level of parental investment for either parent is always lower than that of its partner (Houston et al. 2005, Lessells 2006). This sexual conflict results from the fact that the cost of parental investment (either gametic or through parental care) is paid by one parent, whereas the benefits of that investment are accrued by both parents.

When confronted with conspicuous eggs, males could be selected to either share in incubation or feed incubating females at the nest, thereby minimizing the amount of time that the nest is left unattended with its visually conspicuous contents. A third option is also available to males: resistance, by partial or complete reduction in parental investment. For many species, however, the relative benefits of resistance would be lower than the cost of increasing the level of investment in the current clutch because other mating opportunities in the current breeding season are unlikely (in species with a single clutch per year or with a low breeding density), or because investing in current reproduction is more beneficial than saving energy for future reproductive efforts (in species with low survivorship or in which mate-searching effort is high). It is important to note that although resistance to manipulation is a reasonable alternative in certain breeding strategies, the initial evolution of manipulative behavior depends on the costs and benefits associated with the manipulation itself and not on the resistance of manipulation (Lessells 2006). Moreover, although manipulation of parental investment is believed to be rare because of large opportunity costs associated with manipulating a mating partner (e.g., time lost from other activities that would increase fitness) and because manipulation itself may be difficult (Lessells 2006), female birds have the ability to alter egg and clutch characteristics, thereby providing a mechanism for the direct manipulation of males into providing additional care (Schwabl 1996, Smith and Härdling 2000, Komdeur et al. 2002, Groothuis et al. 2005).

The presence of conspicuous eggs has been bewildering because it is difficult to imagine why a female would lay conspicuous eggs if this behavior is damaging to its partner and increases predation risk to its own clutch. However, theoretical models have shown that damaging mating tactics can be advantageous in general (Johnstone and Keller 2000), especially if direct manipulation can create a situation in which the individual's partner will invest more (Lessells 2006). In some situations, it can prove advantageous for an individual to handicap itself if that behavior results in compensatory effort from its partner (Barta et al. 2002, Houston et al. 2005). For example, a female may elicit more care from its partner if it produces a clutch size beyond its optimum, leaving its own energetic resources too low to sufficiently care for the offspring (Smith and Härdling 2000). Females can also impose conflict load on their partners by increasing the steroid content of eggs, which results in increased begging behavior (Schwabl 1996, Kitaysky et al. 2001, Groothuis et al. 2005) and a potentially greater demand for paternal care (Dickens and Hartley 2007, Dickens et al. 2008). Similarly, males can manipulate females by molting during the nestling period, lowering their foraging ability and forcing females to compensate with higher levels of investment than would otherwise be optimal for them (Hemborg 1999). In some species, sexual conflict is so intense that one or both partners may desert their clutch, and thereby cause the death of all offspring because they skirted their parental duties (Pogány et al. 2008, Eldegard and Sonerud 2009). A recent comparative analysis showed that sexual conflict may even explain the evolution of mating systems and parental care in shorebirds (Thomas and Székely 2005). Considering the magnitude of existing empirical and theoretical work on sexual conflict, a blackmail mechanism for conspicuous egg color seems plausible.

If males respond to conspicuous eggs by sharing in incubation or by feeding females during incubation, this could reduce the risk of nest predation in two ways. First and most obviously, the conspicuous eggs would be concealed from the view of potential predators. Second, the increased nest attendance can lead to higher and more consistent egg temperatures (Martin et al. 2007), a shorter incubation period (Lifjeld and Slagsvold 1986, Nilsson and Smith 1988, Martin et al. 2007) and lower total predation risk (Bosque and Bosque 1995). More optimal incubation temperatures should also increase the quality or condition of offspring (Vleck et al. 1980, Booth 1987, Hepp et al. 2006). Consequently, both parents could experience direct fitness gains from increased male effort during incubation. Furthermore, this increase in offspring quality could result in high levels of investment during the nestling period because males should invest more in higher-quality offspring (Leonard and Horn 1996).

PREDICTIONS AND CONSEQUENCES OF THE BLACKMAIL HYPOTHESIS

The first prediction of the blackmail hypothesis is that in species with conspicuous eggs, parents should spend more time concealing their eggs. In species with uniparental male care, this would be accomplished by an increase in the amount of time that the male spends incubating. In species with biparental care, the mode of concealment should depend on the relative conspicuousness of male and female plumage: where males are drab, they could help either by incubating or by feeding females during incubation; where males are more colorful than females, they should help mainly via incubation feeding. That is, we do not expect conspicuous males to sit on conspicuous eggs, because this would be just as costly from a visual-detection standpoint. Previous work has shown that incubation feeding is beneficial to the female (Smith et al. 1989) and energetically expensive for the male (Lifjeld and Slagsvold 1986), which makes it a likely currency for manipulation.

A second prediction is that species with conspicuous eggs should have shorter incubation periods (controlling for biologically relevant factors) because of the higher, more consistent incubation temperature associated with keeping eggs covered. Interestingly, dramatically low predation risk, compared with that in species with cryptic eggs, might not be expected to result from blackmail driven nest attendance: visual conspicuousness of nest contents is offset by high rates of nest attendance in blackmail species and offset by egg crypsis in non-blackmail species.

A third prediction is that conspicuous egg coloration should be more common in species that are more susceptible to visually oriented predators or parasites. There is already support at the family level for the idea that conspicuous eggs are laid in conspicuous nests (Götmark 1993), and a recent review that controlled for the influence of shared ancestry showed that blue egg coloration is more prevalent in open-cup nests, which are at higher risk of nest predation than cavity nests (Kilner 2006). In nest-building species, the nest itself may also influence conspicuousness to predators (Solís and de Lope 1995). It seems reasonable to assume, however, that the active or passive detection of a nest with conspicuous contents would be more likely than the detection of a nest with cryptic contents (Yahner and Mahan 1996, Svagelj et al. 2003).

A fourth prediction concerns brood parasitism. Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") are generalist brood parasites with hundreds of host species, most of which are smaller than cowbirds in adult body size (Friedmann and Kiff 1985). This size difference makes it difficult for hosts to physically prevent cowbirds from laying eggs in their nests (Ellison and Sealy 2007). In a detailed study of a common small-bodied host, the Yellow Warbler (*Dendroica petechia*), high levels of nest attendance by host females did not prevent a cowbird from laying its parasitic egg, but it usually prevented the cowbird's normal behavior of removing a host egg in association with parasitic laying (Tewksbury et al. 2002). In other words, nest attendance had no effect on parasitism, but it prevented a reduction in host clutch size. If cowbirds respond similarly to nest attendance in other host species, we can predict a consequence of the increased nest attendance that should result from conspicuous-egg blackmail: across species of cowbird hosts, the difference in the number of host eggs in parasitized and unparasitized nests should be smaller in species with conspicuous eggs.

Our final prediction is that as a consequence of the risk associated with conspicuous eggs that are left exposed, species with conspicuous eggs should begin the incubation period earlier to keep their nest contents concealed. Thus, incubation or egg shading in these species are more likely to begin when the antepenultimate or penultimate egg is laid.

CONSISTENT EXAMPLES

Our goal in this section is to generate enough curiosity that readers might be encouraged to pursue robust tests of the blackmail hypothesis, through modeling, experiments, or comparative analyses. To that end, we offer several examples of studies that appear to be consistent with the blackmail hypothesis.

One intriguing example comes from an experimental study of nest attendance by Mourning Doves (*Zenaida macroura*), a sexually monochromatic species in which males provide most of the daytime incubation (Baicich and Harrison 1997). Westmoreland and Best (1986) compared the fates of continually incubated nests and intermittently incubated nests (achieved by deliberately flushing the incubating bird), crossed with a second factor of eggs being either naturally white or artificially colored to be more cryptic. They found that naturally colored white eggs were depredated significantly more than cryptic eggs in nests with intermittent incubation; however, there was no difference between naturally colored and cryptic eggs when both were continually incubated (Westmoreland and Best 1986). Nest concealment, nest height, relative light intensity, and age of eggs at discovery did not differ among the treatments. Interestingly, 85% of clutch failures resulted from visually oriented avian nest predators. The authors suggested that columbids may have evolved constant incubation in response to their conspicuous nest contents (Westmoreland and Best 1986). Interestingly, subsequent work has shown that Columbiformes have a shorter incubation period than would be predicted by body weight (Westmoreland et al. 1986).

A second form of consistent evidence comes from studies of nest attentiveness, mate-feeding behavior, and risk of nest predation. In a comparative analysis, incubation feeding was negatively related to observed nest predation rates in open-cup-nesting species (Martin and Ghalambor 1999). Although egg conspicuousness was not considered in the analysis, the underlying phenomenon may be that incubation feeding allows a cryptic female to spend more time covering conspicuous eggs. In general, there is strong evidence that female nest attentiveness is positively related to male incubation feeding in several species (von Haartman 1958, Lyon and Montgomerie 1985, Moreno and Carlson 1989, Smith et al. 1989, Hałupka 1994). These findings may explain how male help via incubation or incubation feeding in open-cup nests can mitigate the cost of conspicuous nest contents by increasing nest attendance when the risk of predation is high.

A third point of interest comes from tests of the sexual-signaling hypothesis. Several studies have found correlations between egg color and male feeding of nestlings (Moreno et al. 2006b, Hanley et al. 2008, Soler et al. 2008). Such data are consistent with the sexual-signaling hypothesis but also with the blackmail hypothesis. As described earlier, increased incubation attendance (caused by a sexual-signaling mechanism or by blackmail) can lead to better conditions for embryonic development and thus to higher-quality nestlings. Consequently, males that were blackmailed into helping keep conspicuous eggs covered during incubation might then be selected to increase their effort to feed the resulting high-quality brood (Leonard and Horn 1996). This relationship between egg color and paternal care of nestlings should be thought of not as a direct effect of blackmail but as an optimal male strategy if incubation feeding leads to an increase in chick quality.

BROADER IMPLICATIONS

Although we explored the blackmail hypothesis as a way to explain conspicuous egg coloration, and we recognize that blackmail could also operate in non-avian species with conspicuous eggs, the hypothesis itself need not be this limited in scope. There may also be implications for egg coloration in some species of brood parasites. If male songbirds provide more incubation care for nests with conspicuous eggs, a blackmail mechanism might provide a selective advantage to conspicuous eggs of brood parasites. For example, despite extensive variation in the coloration and pattern of host eggs, the eggs of the Bronzed Cowbird (*Tangavius aeneus*) are immaculate; likewise, Shiny Cowbirds (*M. bonariensis*) often lay immaculate eggs (Lowther 1995, Baicich and Harrison 1997, Lowther and Post 1999). This absence of egg mimicry has often been attributed to a limited history of host–parasite coevolution: hosts that have not evolved egg rejection and parasites that have not experienced selection for egg mimicry (Davies 2000). Yet even if hosts are under pressure to evolve egg rejection, it is possible that a blackmail response could cause an increase in incubation attendance at cryptic-egg nests that have been parasitized by cowbirds with conspicuous eggs. In other words, there may be fewer obstacles to the evolution of increased nest attendance (via blackmail) than to the evolution of egg recognition and rejection behavior, particularly if host species also benefit through decreased egg ejection by the parasite as outlined in our fourth prediction. In the long run, however, the evolution of rejection would still be advantageous in that it would eliminate the high costs associated with rearing the brood-parasitic nestling (Dearborn and Lichtenstein 2002).

Another extension of the blackmail hypothesis is that threats of egg destruction need not be based solely on conspicuousness to enemies: a similar threat may be incurred through the use of precarious nest sites, as documented in White Terns (*Gygis alba*), which usually lay their egg on a small branch without building a nest (Niethammer and Patrick 1998). In this situation, increased nest attendance reduces the chance that wind or contact will cause the egg to fall and break. Similarly, blackmail may be instigated through egg placement in potoos, which lay a single conspicuous white egg precariously in a slight depression of a branch or stump (Stiles and Skutch 1989).

SYNTHESIS

Despite decades of interest and inquiry, the evolution of conspicuous eggs remains something of a mystery. Our hypothesis proposes that conspicuous egg coloration may evolve as a form of sexual conflict. Thus, conspicuous eggs, which require higher parental investment to remain concealed, may be at a selective advantage in some species. The blackmail hypothesis may help explain interspecific variation in male incubation feeding in birds (Ricklefs 1974, Jawor and Breitwisch 2006). Moreover, a blackmail outlook on parental care might be expanded to other seemingly maladaptive traits such as precarious egg placement and nonmimetic brood-parasitic eggs.

It is important to note that blackmail and other hypotheses for the evolution of conspicuous egg coloration are not mutually exclusive. Across species, a particular trait can vary in the adaptive function it serves or in the constraints that limit its evolution, and conspicuous eggs certainly could be present in different species for different reasons (Kilner 2006). Indeed, multiple hypotheses may even reinforce each other in certain situations. For example, if paternal investment and egg conspicuousness have increased through blackmail, this mechanism may have produced enough intraspecific variation for other selection pressures to operate in some species (e.g., evaluation of relative female quality).

We are not suggesting that risk associated with egg detectability explains all occurrences of conspicuous eggs, but simply that it is a plausible hypothesis in certain situations. This idea presents a testable scenario for the presence of conspicuous egg coloration. In addition to perhaps explaining intriguing nesting behaviors in birds, this idea creates a new avenue for egg color research and may explain, at least in part, seemingly maladaptive egg coloration, which has perplexed naturalists for more than 100 years.

Acknowledgments

We thank M. Abdellah, I. Bobeica, D. Bradley, J. Cuthbert, A. Mistakidis, E. Schneider, and A. Zahavi for insightful discussions on this topic and comments on the manuscript. We appreciate the comments and feedback we received from K. McGraw, S. Sealy, and anonymous reviewers. We also thank R. Payne, R. Storer, and J. Hinshaw for providing access to the egg collection at the University of Michigan Museum of Zoology.

Literature Cited

Baicich, P. J., and C. J. O. Harrison. 1997. A Guide to the Nests, Eggs, and Nestlings of North American Birds, 2nd ed. Academic Press, San Diego, California.

Bakken, G. S., V. C. Vanderbilt, W. A. Buttemer, and W. R. Dawson. 1978. Avian eggs: Thermoregulatory value of very high near-infrared reflectance. Science 200:321–323.

Barta, Z. N., A. I. Houston, J. M. McNamara, and T. Székely. 2002. Sexual conflict about parental care: The role of reserves. American Naturalist 159:687–705.

Bertram, B. C. R., and A. E. Burger. 1981. Are Ostrich *Struthio camelus* eggs the wrong colour? Ibis 123:207–210.

Booth, D. T. 1987. Effect of temperature on development of Mallee Fowl *Leipoa ocellata* eggs. Physiological Zoology 60:437–445.

Bosque, C., and M. T. Bosque. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. American Naturalist 145:234–260.

Cabot, J. 1992. Tinamiformes. Pages 111–138 *in* Handbook of the Birds of the World, vol. 1: Ostrich to Ducks (J. del Hoyo, A. Elliott, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.

Castilla, A. M., A. A. Dhondt, R. Díaz-Uriarte, and D. Westmoreland. 2007. Predation in ground-nesting birds: an experimental study using natural egg-color variation. ACE-ÉCO 2:2.

Cott, H. B. 1948. Edibility of the eggs of birds. Nature 161:8–11.

Davies, N. B. 2000. Cuckoos, Cowbirds, and Other Cheats. T & AD Poyser, London.

Dearborn, D. C., and G. Lichtenstein. 2002. Begging behaviour and host exploitation in three species of parasitic cowbirds. Pages 361–387 *in* The Evolution of Begging: Competition, Cooperation, and Communication (J. Wright and M. Leonard, Eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Dickens, M., D. Berridge, and I. R. Hartley. 2008. Biparental care and offspring begging strategies: Hungry nestling Blue Tits move towards the father. Animal Behaviour 75:167–174.

Dickens, M., and I. R. Hartley. 2007. Differences in parental food allocation rules: Evidence for sexual conflict in the Blue Tit? Behavioral Ecology 18:674–679.

Eldegard, K., and G. A. Sonerud. 2009. Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. Proceedings of the Royal Society of London, Series B 276:1713–1721.

Ellison, K., and S. G. Sealy. 2007. Small hosts infrequently disrupt laying by Brown-headed Cowbirds and Bronzed Cowbirds. Journal of Field Ornithology 78:379–389.

Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41:315–352.

Friedmann, H., and L. F. Kiff. 1985. The parasitic cowbirds and their hosts. Proceedings of the Western Foundation of Vertebrate Zoology 2:225–304.

Götmark, F. 1992. Blue eggs do not reduce nest predation in the Song Thrush, *Turdus philomelos*. Behavioral Ecology and Sociobiology 30:245–252.

Götmark, F. 1993. Conspicuous nests may select for non-cryptic eggs: A comparative study of avian families. Ornis Fennica 70: 102–105.

Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. Proceedings of the Royal Society of London, Series B 205:581–598.

Groothuis, T. G. G., W. Müller, N. von Engelhardt, C. Carere, and C. Eising. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. Neuroscience and Biobehavioral Reviews 29:329–352.

Hałupka, K. 1994. Incubation feeding in Meadow Pipit *Anthus pratensis* affects female time budget. Journal of Avian Biology 25:251–253.

Hanley, D., and S. M. Doucet. 2009. Egg coloration in Ring-billed Gulls (*Larus delawarensis*): A test of the sexual signaling hypothesis. Behavioral Ecology and Sociobiology 63:719–729.

Hanley, D., G. Heiber, and D. C. Dearborn. 2008. Testing an assumption of the sexual-signaling hypothesis: Does blue-green egg color reflect maternal antioxidant capacity? Condor 110:767–771.

Hemborg, C. 1999. Sexual differences in moult–breeding overlap and female reproductive costs in Pied Flycatchers, *Ficedula hypoleuca*. Journal of Animal Ecology 68:429–436.

Hepp, G. R., R. A. Kennamer, and M. H. Johnson. 2006. Maternal effects in Wood Ducks: Incubation temperature influences incubation period and neonate phenotype. Functional Ecology 20:307–314.

Holyoak, D. 1969. The function of the pale egg colour of the jackdaw. Bulletin of the British Ornithologists' Club 89:159.

Houston, A. I., T. Székely, and J. M. McNamara. 2005. Conflict between parents over care. Trends in Ecology and Evolution 20:33–38.

Jawor, J. M., and R. Breitwisch. 2006. Is mate provisioning predicted by ornamentation? A test with Northern Cardinals (*Cardinalis cardinalis*). Ethology 112:888–895.

Johnstone, R. A., and L. Keller. 2000. How males can gain by harming their mates: Sexual conflict, seminal toxins, and the cost of mating. American Naturalist 156:368–377.

Kilner, R. M. 2006. The evolution of egg colour and patterning in birds. Biological Reviews 81:383–406.

Kitaysky, A. S., J. C. Wingfield, and J. F. Piatt. 2001. Corticosterone facilitates begging and affects resource allocation in the Black-legged Kittiwake. Behavioral Ecology 12:619–625.

Komdeur, J., P. Wiersma, and M. Magrath. 2002. Paternal care and male mate-attraction effort in the European Starling is adjusted to clutch size. Proceedings of the Royal Society of London, Series B 269:1253–1261.

Krist, M., and T. Grim. 2007. Are blue eggs a sexually selected signal of female Collared Flycatchers? A cross-fostering experiment. Behavioral Ecology and Sociobiology 61:863–876.

Krüger, O., J. Lindström, and W. Amos. 2001. Maladaptive mate choice maintained by heterozygote advantage. Evolution 55: 1207–1214.

Lack, D. 1958. The significance of the colour of turdine eggs. Ibis 100:145–166.

Lancaster, D. A. 1964. Life history of the Boucard Tinamou in British Honduras. Part II: Breeding biology. Condor 66:253–276.

Leonard, M., and A. Horn. 1996. Provisioning rules in Tree Swallows. Behavioral Ecology and Sociobiology 38:341–347.

Lessells, C. M. 2006. The evolutionary outcome of sexual conflict. Philosophical Transactions of the Royal Society of London, Series B 361:301–317.

Lifjeld, J. T., and T. Slagsvold. 1986. The function of courtship feeding during incubation in the Pied Flycatcher *Ficedula hypoleuca*. Animal Behaviour 34:1441–1453.

López-Rull, I., P. Celis, and D. Gil. 2007. Egg colour covaries with female expression of a male ornament in the Spotless Starling (*Sturnus unicolor*). Ethology 113:926–933.

Lowther, P. E. 1995. Bronzed Cowbird (*Molothrus aeneus*). *In* The Birds of North America, no. 144 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Lowther, P., and W. Post. 1999. Shiny Cowbird (*Molothrus bonariensis*). *In* The Birds of North America, no. 399 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Lyon, B. E., and R. D. Montgomerie. 1985. Incubation feeding in Snow Buntings: Female manipulation or indirect male parental care? Behavioral Ecology and Sociobiology 17:279–284.

Magige, F. J., B. Moe, and E. Røskaft. 2008. The white colour of the Ostrich (*Struthio camelus*) egg is a trade-off between predation and overheating. Journal of Ornithology 149:323–328.

Martin, T. E., S. K. Auer, R. D. Bassar, A. M. Niklison, and P. Lloyd. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. Evolution 61:2558–2569.

Martin, T. E., and C. K. Ghalambor. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation. American Naturalist 153:131–139.

McAldowie, A. M. 1886. Observations on the development and the decay of the pigment layer on birds' eggs. Journal of Anatomy and Physiology 20:225–237.

Montevecchi, W. A. 1976. Field experiments on adaptive significance of avian eggshell pigmentation. Behaviour 58:26–39.

Moreno, J., and A. Carlson. 1989. Clutch size and the costs of incubation in the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scandinavica 20:123–128.

Moreno, J., E. Lobato, J. Morales, S. Merino, G. Tomás, J. Martínez-de la Puente, J. J. Sanz, R. Mateo, and J. J. Soler. 2006a. Experimental evidence that egg color indicates female condition at laying in a songbird. Behavioral Ecology 17:651–655.

Moreno, J., J. Morales, E. Lobato, S. Merino, G. Tomás, and J. Martínez-de la Puente. 2005. Evidence for the signaling function of egg color in the Pied Flycatcher *Ficedula hypoleuca*. Behavioral Ecology 16:931–937.

Moreno, J., J. Morales, E. Lobato, G. Tomás, and J. Martínez-de la Puente. 2006b. More colourful eggs induce a higher relative paternal investment in the Pied Flycatcher *Ficedula hypoleuca*: A cross-fostering experiment. Journal of Avian Biology 37:555–560.

Moreno, J., and J. L. Osorno. 2003. Avian egg colour and sexual selection: Does eggshell pigmentation reflect female condition and genetic quality? Ecology Letters 6:803–806.

Moreno, J., J. L. Osorno, J. Morales, S. Merino, and G. Tomás. 2004. Egg colouration and male parental effort in the Pied Flycatcher *Ficedula hypoleuca*. Journal of Avian Biology 35:300–304.

Muñoz, A. R., M. Altamirano, F. Takasu, and H. Nakamura. 2007. Nest light environment and the potential risk of Common Cuckoo (*Cuculus canorus*) parasitism. Auk 124:619–627.

Niethammer, K. R., and L. B. Patrick. 1998. White Tern (*Gygis alba*). *In* The Birds of North America Online, no. 371 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Nilsson, J.-Å., and H. G. Smith. 1988. Incubation feeding as a male tactic for early hatching. Animal Behaviour 36:641–647.

Pogány, Á., I. Szentirmai, J. Komdeur, and T. Székely. 2008. Sexual conflict and consistency of offspring desertion in Eurasian Penduline Tit *Remiz pendulinus*. BMC Evolutionary Biology 8:242.

Reynolds, S. J., G. R. Martin, and P. Cassey. 2009. Is sexual selection blurring the functional significance of eggshell coloration hypotheses? Animal Behaviour 78:209–215.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–297 *in* Avian Energetics, no. 15 (R. A. Paynter, Ed.). Nuttall Ornithological Club, Cambridge, Massachusetts.

Schwabl, H. 1996. Maternal testosterone in the avian egg enhances postnatal growth. Comparative Biochemistry and Physiology A 114:271–276.

Siefferman, L., K. J. Navara, and G. E. Hill. 2006. Egg coloration is correlated with female condition in Eastern Bluebirds (*Sialia sialis*). Behavioral Ecology and Sociobiology 59:651–656.

Smith, H. G., and R. Härdling. 2000. Clutch size evolution under sexual conflict enhances the stability of mating systems. Proceedings of the Royal Society of London, Series B 267:2163–2170.

Smith, H. G., H. Källander, J. Hultman, and B. Sanzén. 1989. Female nutritional state affects the rate of male incubation feeding in the Pied Flycatcher *Ficedula hypoleuca*. Behavioral Ecology and Sociobiology 24:417–420.

Soler, J. J., C. Navarro, T. Pérez-Contreras, J. M. Avilés, and J. J. Cuervo. 2008. Sexually selected egg coloration in Spotless Starlings. American Naturalist 171:183–194.

Solís, J. C., and F. de Lope. 1995. Nest and egg crypsis in the ground-nesting Stone Curlew *Burhinus oedicnemus*. Journal of Avian Biology 26:135–138.

Stiles, F. G., and A. F. Skutch. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York.

Svagelj, W. S., M. E. Mermoz, and G. J. Fernández. 2003. Effect of egg type on the estimation of nest predation in passerines. Journal of Field Ornithology 74:243–249.

Swynnerton, C. F. M. 1916. On the coloration of the mouths and eggs of birds. II. On the coloration of eggs. Ibis 4:529–606.

Tewksbury, J. J., T. E. Martin, S. J. Hejl, M. J. Kuehn, and J. W. Jenkins. 2002. Parental care of a cowbird host: Caught between the costs of egg-removal and nest predation. Proceedings of the Royal Society of London, Series B 269:423–429.

Thomas, G. H., and T. Székely. 2005. Evolutionary pathways in shorebird breeding systems: Sexual conflict, parental care, and chick development. Evolution 59:2222–2230.

Underwood, T. J., and S. G. Sealy. 2002. Adaptive significance of egg coloration. Pages 280–298 *in* Avian Incubation: Behaviour, Environment, and Evolution (D. C. Deeming, Ed.). Oxford University Press, New York.

Vleck, C. M., D. Vleck, and D. F. Hoyt. 1980. Patterns of metabolism and growth in avian embryos. American Zoologist 20: 405–416.

von Haartman, L. 1957. Adaptation in hole-nesting birds. Evolution 11:339–347.

von Haartman, L. 1958. The incubation rhythm of the female Pied Flycatcher (*Ficedula hypoleuca*) in the presence and absence of the male. Ornis Fennica 35:71–76.

Wallace, A. R. 1889. Darwinism: An Exposition of the Theory of Natural Selection with Some of Its Applications. Macmillan, London.

Westmoreland, D. 2008. Evidence of selection for egg crypsis in conspicuous nests. Journal of Field Ornithology 79:263–268.

Westmoreland, D., and L. B. Best. 1986. Incubation continuity and the advantage of cryptic egg coloration to Mourning Doves. Wilson Bulletin 98:297–300.

Westmoreland, D., L. B. Best, and D. E. Blockstein. 1986. Multiple brooding as a reproductive strategy: Time-conserving adaptations in Mourning Doves. Auk 103:196–203.

Yahner, R. H., and C. G. Mahan. 1996. Effects of egg type on depredation of artificial ground nests. Wilson Bulletin 108:129–136.

Zahavi, A., and A. Zahavi. 1997. The Handicap Principle: A Missing Piece of Darwin's Puzzle. Oxford University Press, New York.

Received 23 February 2009, accepted 26 August 2009
Associate Editor: K. J. McGraw