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Behaviorally Induced Camouflage: A New Mechanism of Avian Egg Protection

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ABSTRACT: When animals potentially occupy diverse microhabitats, how can camouflage be achieved? Here we combine descriptive and experimental methods to uncover a novel form of phenotypic plasticity in the camouflage of bird eggs that may be present in other avian taxa. Soil from the bare substrate adheres to the blue-footed booby's (*Sula nebouxi*'s) pale eggs, which parents manipulate both under and on top of their webs. Analysis of digital images confirmed that dirtiness increases progressively during the first 16 days of the incubation period, making eggs more similar to the nest substrate. Observations of 3,668 single-egg clutches showed that the probability of egg loss declines progressively over the same time frame and then remains low for the rest of the 41-day incubation period. An experiment showed that when chicken eggs are soiled and exposed in artificial booby nests, they are less likely to be taken by Heermann's gulls (*Larus heermanni*) than clean eggs.

Keywords: camouflage, avian eggs, defense, plasticity, predation.

Introduction

Many animal species conceal themselves from attack through camouflage, with traits that are exquisitely shaped, patterned, or colored to prevent detection by a potential predator (Stevens and Merilaita 2011). Camouflage traits function either by allowing the animal to blend into the background on which it rests (background matching) or by reducing edge detection through patterning (disruptive coloration; Cott 1940). Whichever of these mechanisms hides the animal from attack, its success is contingent on a good match between the trait and the habitat in which it is expressed. Since habitats (and camouflage traits) can be highly variable, two possibilities then follow for maximizing camouflage success.

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One way to guarantee that the trait is expressed only in the appropriate environment is if the bearer is somehow confined to that habitat. There may be a genetic correlation between habitat preference and optimal camouflage (Jaenike and Holt 1991), or animals may actively choose the habitat that most effectively confers protection by camouflage (Karpestam et al. 2012; Lovell et al. 2013). In these examples, then, camouflage traits are constitutively expressed, and the match to the habitat may be achieved through genetic correlation or behavioral choice.

An alternative way to link camouflage traits to their appropriate habitat is seen when camouflage is flexibly induced by the environment in which the animal lives. One possibility is that the environment induces the expression of genes that confer the appropriate camouflage traits, as seen in chameleons, for example (Stuart-Fox et al. 2006). An alternative possibility, which we focus on here, is that animals acquire their camouflage behaviorally from the environment (Montgomerie et al. 2001). For example, rock ptarmigan (Montgomerie et al. 2001), spider crabs (Wicksten 1993), marine gastropods (Portmann 1956), and weevils (Gressitt and Samuelson 1968) all mask themselves with environmentally acquired material and so seemingly render themselves cryptic (or, at least, less visible) to predators. Nevertheless, this form of camouflage is relatively little understood because it has not yet been subjected to objective quantification nor exposed to much experimental analysis (but see Brandt and Mahsberg 2002).

Here we describe a novel form of behaviorally induced avian egg camouflage, achieved through the gradual adherence of substrate material to the shell. We use objective techniques to quantify the extent of camouflage and field experiments to assess its adaptive value. Egg coloration is a widespread avian strategy for defending eggs against visually hunting predators, especially in ground-nesting species (Tinbergen et al. 1962; Underwood and Sealy 2002;

Nguyen et al. 2003; Kilner 2006), and it is commonly achieved through the deposition of bilirubin or biliverdin in the eggshell (Kilner 2006; Stoddard et al. 2011). Pigmentation can camouflage eggs by background matching (Stevens and Merilaita 2009a) or disruption of the egg outline (Stevens and Merilaita 2009b), as well as by creating within-clutch color variation that is visually confusing to a potential predator (Hockey 1982; Lloyd et al. 2000). Nevertheless, pigmented egg color and patterning is typically relatively consistent within each female (Kilner 2006), which means that optimal camouflage may be achieved only through a genetic correlation with the microhabitat or through optimal choice of a nest site (Stoddard et al. 2011; Lovell et al. 2013).

By contrast, blue-footed boobies (*Sula nebouxi*) appear to camouflage their eggs by soiling them with some of the substrates on which they nest (Nelson 2005), although whether this constitutes an effective defense against predators is not yet known. Blue-footed boobies nest colonially on horizontal or moderately sloping ground, where they lay clutches of 1–3 eggs in shallow depressions that they scrape into soil or sand with their bills. At the time of laying, their eggs are pale blue due to the presence of biliverdin in the shell, but they fade to a whitish color in a few days (Morales et al. 2010) and often acquire the color of the nest substrate; a few weeks after laying they can be almost indistinguishable from the dark soil they rest on, at least to human eyes. Whereas many birds incubate their eggs with a brood patch located on the breast, blue-footed boobies use their webbed feet. The incubating adult spreads its webs over the clutch resting on the bare substrate or sustains the clutch on top of its webs (Nelson 1978) while periodically rotating the eggs by jostling with its feet or nudging with its bill. This control over contact and friction between eggshells and substrate and over the ventilation and humidity of both, possibly augmented by frequent excreting around the nest scrape, potentially regulates soiling.

During the brief periods when parents leave them exposed, blue-footed booby eggs are sometimes taken by visual predators. At our study site on Isla Isabel in the Mexican Pacific Ocean (lat. 21°52'N, long. 105°54'W), 34% and 70% of eggs were lost from early clutches (laid between December 26 and March 4) and late clutches (laid between March 5 and June 10), respectively (Peña-Álvarez 2009; D'Alba and Torres 2007). Many were taken by Heermann's gulls (*Larus heermanni*), which commonly fly over and walk through the colony, in some cases after clutches were abandoned by parents. During the 41-day incubation period, parents cover their eggs continuously except during incubation changeovers, when they rise up to attack predators and intruding boobies (Nelson 1978; Drummond et al. 1986), and, possibly, when females expose freshly laid eggs to visual inspection by their partners (Morales et al. 2010).

To test the hypothesis that substrate soiling reduces gull predation on booby eggs by camouflaging them, we quantified the change in background matching that occurs over the incubation period and then tested two predictions: (1) that the rate of attack on booby eggs should decline as the incubation period progresses and shells become progressively better matched to the nest background on which they sit and (2) that chicken eggs (similar in size and color to booby eggs) placed experimentally in artificial booby nests should suffer less gull predation when soiled than when clean.

Material and Methods

Study Site

Isla Isabel is a volcanic island mostly covered by tropical deciduous forest of garlic pear (*Crataeva tapia*) and pape-lillo (*Euphorbia schlechtendalli*) trees, to a maximum height of 9 m, and grassland composed of *Trichachne insularis*, *Cyperus ligularis*, and *Cenchrus viridis*. The boobies nest on bare forest floor, mostly under garlic pear trees; on bare patches of sandy soil among bunches of *C. ligularis*; and on beach sand. Nest substrates in forest and grassland are littered to varying degrees with fallen leaves and other organic material. Since 1989, breeding has been monitored annually in two study areas, and all fledglings there have been individually banded (Drummond et al. 2003).

Soiling

A cross-sectional test of soiling over the incubation period was made in 2012 in the forest and grassland of the two study areas. We did not sample from the beach, where the pale yellow sand of nest substrates does not appear to soil booby eggs, which remain whitish throughout the incubation period. Routine monitoring of all nests every 3 days after February 23 allowed us to identify and photograph 109 known-age clutches with two banded parents between February 29 and March 5. Ages of 79 clutches were known because they were laid during monitoring, and ages of 30 clutches were calculated by estimating their lay dates from their hatch dates. With a digital camera, an observer photographed each nest substrate and clutch from a height of 45 cm at a vertical angle between 09:00 and 17:00 under natural lighting, in his own shadow. Eggs were weighed with an Ohaus Navigator balance (1,200 g × 0.1 capacity) and measured (length and width) with a vernier, and nest substrates were categorized by visual inspection as soil, soil plus gravel, or soil with fragments of dead leaves. Subsequently, egg volumes were estimated as $0.51 \times \text{length} \times \text{width}^2$ (Hoyt 1979); ages (days) of eggs were calculated from their laying dates or their hatching dates, on the basis of an

average incubation period of 41 days (Drummond et al. 1986), and parental ages were extracted from a database.

We quantified eggshell dirtiness in each photograph using ImageJ software. To estimate the proportion of each egg covered with dirt/substrate material, we used the image from the camera's green sensor only. The green sensor roughly approximates the avian luminance channel (Spottiswoode and Stevens 2010), which is likely important for achromatic visual tasks related to pattern and texture detection (Jones and Osorio 2004). We thresholded each image such that the dirty area of the egg was selected; we then measured the proportion of the egg's total area covered with dirt. The observer who photographed the clutches and quantified the eggs' dirtiness was masked to information about their ages. To determine whether dirtiness increases with egg age while controlling for type of substrate, egg age, quadratic egg age, parental ages, quadratic parental ages, egg volume, clutch size, and study area, we built a generalized linear mixed model (GLMM) with normal error distribution and identity link function, with nest identity as a random variable. Quadratic parental ages were included to test for improvement and decline in dirtiness with age and experience. We also included the interaction between egg age and type of substrate and between quadratic egg age and type of substrate to test whether substrate quality affects soiling. We simplified this and all other models of the study by sequentially dropping nonsignificant ($P > .05$) interactions and main terms until we obtained minimal adequate models including only significant interactions and variables.

Predation over the Incubation Period

From a long-term database we obtained survival until hatching of all 3,668 one-egg clutches laid late in the season (between March 4 and June 10) in the study areas over a 30-year period (1981–2011). These late clutches were inspected every 3 or 6 days between laying and hatching (details are provided in Drummond et al. 2003). To examine in detail the rate of egg loss with respect to the duration of incubation, we divided the 41 days of incubation into eight 5-day intervals (including the 41st day in the last interval) and calculated the proportion of eggs lost in each of the eight intervals, taking into account only eggs present at the start of each interval. We compared the proportions of eggs lost among the eight intervals using a G test.

Predation on Soiled versus Clean Eggs

Between March 25 and April 3, 2012, artificial nests were created in forest and grassland outside the two study areas, none of them closer than 5 m to the nearest gull and booby nests. In forest, they were placed within 30 m of the for-

est edge, the zone used by boobies for nesting and overflowed by gulls. Nests were created by manually scraping and molding the soil into the form of a natural booby nest.

A white chicken (*Gallus gallus domesticus*) egg was placed in each artificial nest. In comparison with the 109 booby eggs measured in the soiling analysis, a random sample of 10 chicken eggs were shorter (booby: 60.86 ± 3.55 mm; chicken: 57.39 ± 2.04 mm; $t_{117} = 3.04$, $P < .002$; mean \pm standard deviation, independent t test) and wider (booby: 41.33 ± 1.34 mm; chicken: 43.45 ± 0.98 mm; $t_{117} = 4.87$, $P < .0001$) but similar in volume (booby: 53.00 ± 5.25 mm³; chicken: 55.33 ± 3.21 mm³; $t_{117} = 1.37$, $P = .171$). Experimental eggs were soiled the day before the experiment by briefly rubbing damp soil from the ground near booby nests onto their shells until they resembled naturally soiled booby eggs. The proportion of eggshell covered with soil was 0.894 ± 0.028 ($n = 6$), similar to the dirtiest booby eggs aged 3–40 days in the soiling analysis. Clean eggs were simply handled and rubbed in the absence of soil.

In each of 25 tests (13 in forest and 12 in grassland) at 25 different locations along a 1.2-km transect, we placed four soiled eggs and four clean eggs in eight artificial nests separated approximately 15 m from each other (1 egg per nest; total of 100 soiled and 100 clean eggs). Two seated observers wearing camouflage capes recorded behavior at four nests each, including two with clean eggs and two with soiled eggs, assigned randomly. After unmasking the 8 eggs by pulling strings attached to camouflage cloth patches, the observers registered predation events over 2 h from a distance of roughly 12 m while minimizing their movements. Tests were conducted during 07:00–10:30, 10:30–13:30, or 15:00–18:00. Some eggs were attacked and destroyed (but not eaten) by boobies, and the observers registered the timing of these attacks and the perpetrators' sex and breeding status: solitary, courting, incubating, or brooding. Sex was identified by voice: females grunt and males whistle.

Using two independent models, we analyzed the incidence of predation by gulls on eggs that were not attacked by boobies and of destruction by boobies of eggs that were not predated by gulls. We built GLMMs with binomial error distribution and logit link (Crawley 2003) to test whether the probability of predation by gulls or destruction by boobies was affected by egg color (soiled or clean), habitat (forest or grassland), and time of day, as well as the interaction between egg color and habitat. Test number was included as a random effect. In addition, to test whether latency to suffer predation was greater for soiled eggs than clean eggs, we used another GLMM with normal error distribution and identity link, including the same independent variables and random effect. Latency to predation was measured as the time (≤ 120 min) from the start of the test until the egg was taken by a predator.

All models in this study were fitted using R (ver. 2.15.0; R Development Core Team 2012). All data are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.76bf0> (Mayani-Parás et al. 2015).

Results

Soiling

The proportion of the booby eggshell that was covered with soil increased both linearly ($F_{1,28} = 60.90$, $P < .0001$) and quadratically ($F_{1,28} = 20.15$, $P = .0001$) with egg age (figs. 1A, 2). A follow-up piecewise analysis (Crawley 2007) of the quadratic effect showed that dirtiness increased steeply during the first 4 days then more slowly through day 16 (0–4 days of age: $F_{1,10} = 29.12$, $P = .0003$; 5–16 days of age: $F_{1,7} = 30.43$, $P = .0009$), after which it remained stable until the end of incubation (17–40 days of age: $F_{1,1} = 1.93$, $P = .397$). No other factors or interactions were significant.

Predation over the Incubation Period

Fully 47% of the 3,668 eggs in late clutches were lost in the first 5 days after laying, after which the proportion lost in each subsequent 5-day interval decreased progressively through age 15 days, beyond which the rate of loss was low and stable, with no loss higher than 20% in any interval ($G_7 = 868.12$, $P < .0001$; fig. 1B).

Predation on Soiled versus Clean Eggs

Gulls flying over the colony either swooped to snatch an egg on the wing and flew off with it or landed and ate the egg at the nest or departed with it, walking or flying, just as they commonly do with booby eggs in natural nests. Gulls that remained in sight ate the eggs with which they departed. On only two occasions did a gull remain to take a second egg. Because we could not identify individual gulls, we could not tell whether any individuals took more than one experimental egg.

Gulls took 56 of the 183 chicken eggs that were not destroyed by boobies, including 34 clean eggs and 22 soiled eggs. Soiled eggs were less likely to be taken than clean ones ($\chi^2_1 = 8.984$, $P = .003$), regardless of whether they were in forest or grassland (color \times habitat: $\chi^2_1 = 0.608$, $P = .435$; fig. 3). Predation was more likely in grassland than in forest (habitat: $\chi^2_1 = 4.831$, $P = .028$), but time of day had no effect ($\chi^2_2 = 0.971$, $P = .647$). Predation latency was not significantly affected by any analyzed variable, including egg color.

On 17 occasions, boobies that were departing from or returning to their territories walked toward an artificial nest and either pecked the egg until it broke or carried and tossed it. Afterward, they resumed their journeys. Of 144 eggs that were not predated by gulls, 17 were destroyed by boobies, including 14 clean eggs and 3 soiled eggs. Boobies were more likely to destroy clean eggs than soiled eggs ($\chi^2_1 = 10.053$, $P = .001$) regardless of habitat (color \times habitat: $\chi^2_1 = 0.1$, $P = .752$). Neither habitat ($\chi^2_2 = 1.33$, $P =$

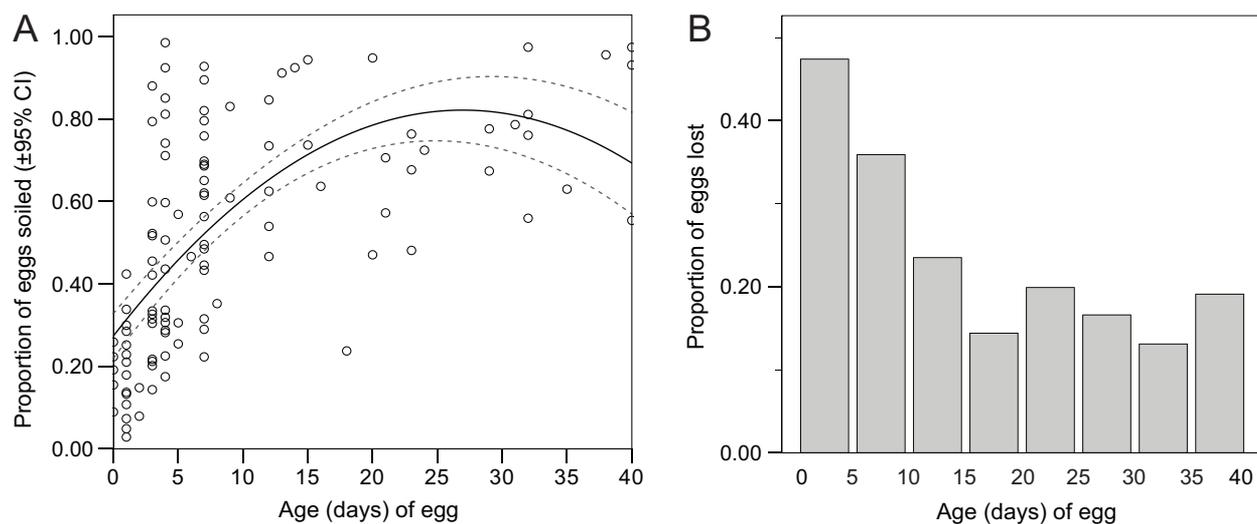


Figure 1: Increase in dirtiness and decrease in loss of booby eggs over the incubation period. *A*, A significant increase in dirtiness occurred over the first 16 days ($N = 109$ eggs in 2012). *B*, The proportion of eggs lost declined over a similar period ($N = 3,668$ single-egg clutches laid between 1981 and 2011). CI = confidence interval.



Figure 2: Blue-footed booby eggs at different ages.

.514) nor time of day ($\chi^2_1 = 1.415$, $P = .234$) affected the probability of destruction. Males carried out 82% of booby attacks, and 70% of these were courting or solitary males with a territory but no clutch.

Discussion

We found that blue-footed boobies changed the color of their eggs during incubation, darkening them from pale blue and whitish by transferring soil from the nest substrate onto the shell during foot-mediated incubation. There was a pronounced change in egg dirtiness over the first 4 days of incubation, followed by more gradual darkening over the next 12 days of the incubation period. After the 16th day, dirtiness was stable (fig. 1A).

We investigated whether soiling of eggs in this way is a flexible mechanism for conferring camouflage, adaptively defending the pale-colored eggs against attack by predators when the clutch is otherwise highly visible against a dark nest background. Observations gathered at more than

3,668 late-season nests provided correlational evidence consistent with this view. Clutches were most vulnerable to attack in the days immediately following laying (fig. 1B), when eggs were still relatively pale (fig. 1A). The rate of attack declined thereafter, stabilizing at a relatively low level around 15 days after incubation (fig. 1B)—almost exactly the same time that the extent of egg dirtiness also became stable (fig. 1A). Although these correlations are consistent with the possibility that the gradual soiling of eggs reduces their detectability by potential predators, other explanations should be considered. One possibility is that eggs are exposed to predators more frequently in the period immediately following laying. In the hours after laying an egg, a female booby sometimes stands over it rather than covering it with her feet, as if in motivational conflict or possibly to expose it to her partner (Morales et al. 2010), and both sexes sometimes temporarily abandon newly laid eggs when disturbed and occasionally abandon fresh clutches completely (Nelson 1978). Uncovered and unguarded eggs can be quickly detected and taken by overflying gulls, and such predation could account for some of the 47% of single eggs in late clutches that disappear during the first 5 days after laying. However, uncovering and temporarily abandoning eggs seems to be confined to the hours or possibly a few days after laying. These lapses appear far less frequent after a pair has established an incubation routine and are unlikely to explain the elevated loss of eggs observed at ages 5–15 days.

A second possibility is that the decline in attack by predators is due not to increased egg camouflage but to other factors correlated with the age of the egg. For example, parents might care for and defend eggs better as their value increases (i.e., residual required investment decreases) or as male caretakers possibly desist in their extrapair activities.

To test whether soiling itself caused a decline in egg conspicuousness and so reduced the rate of predator attack, we experimentally dirtied white chicken eggs and exposed them to attack by predators, thus removing any potentially confounding effects of parental behavior. We found that chicken eggs that were soiled were 10%–20% less likely than clean chicken eggs to be predated by gulls when they were presented in open artificial nests in either

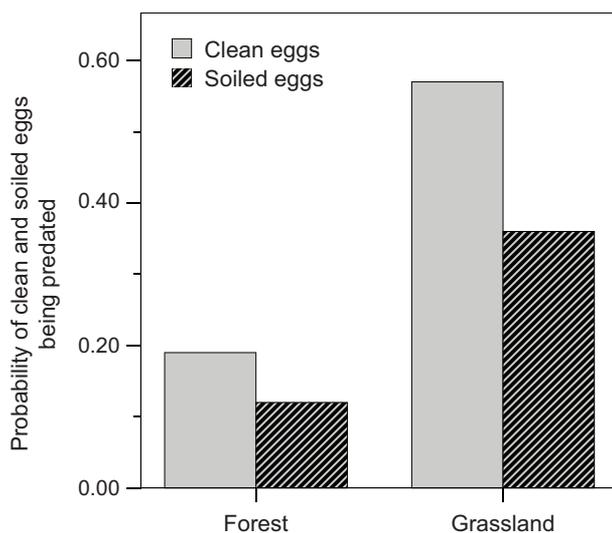


Figure 3: Probability of clean and soiled chicken eggs being predated by gulls in artificial nests in forest and grassland ($N = 183$ eggs).

forest or grassland (fig. 3), strongly suggesting that egg soiling caused the decline in predation observed at natural nests.

In our experiment, egg soiling camouflaged eggs from both predatory gulls and passing boobies. However, all conspecific egg destruction observed in natural contexts was directed at freshly laid eggs (H. Drummond, unpublished data), so—on Isla Isabel at least—soiling probably protects eggs against predatory gulls much more often than against conspecifics competing for space. In general, experimental eggs were less likely to be attacked by predators in the forest than in the grassland (fig. 3), perhaps because visual detection by overflying predators was complicated in the forest by shadows and poor illumination and was obstructed by the canopy. Furthermore, egg soiling at natural nests was associated with an overall decline in attack rate of about 20% (fig. 1B), which was slightly greater than we detected experimentally. This might be because possible increases in parental nest defense behavior additionally and independently contributed to reduce egg loss as the incubation period progressed.

Why do boobies camouflage their eggs by using behavioral techniques rather than pigmentation? A previous phylogenetic analysis suggests that brown egg pigmentation has been secondarily lost by the Sulidae (Kilner 2006; although this conclusion comes with the caveat that the result is only as sound as the molecular phylogeny on which it is based), which in turn suggests that the current white/pale blue shell coloration is adaptive at least some of the time. By darkening egg color behaviorally, boobies can potentially exploit a greater range of nest substrates than might otherwise be possible because the extent of egg camouflage can be flexibly manipulated to suit the local nest environment. Perhaps this is particularly important for a colonial island-nesting bird that experiences intense competition for nest sites. Seen like this, egg camouflage by soiling is another example of a phenotypically plastic trait that is potentially adaptive because it enables populations to persist in diverse or changeable environments (Ghalambor et al. 2007). We predict that other species should exhibit similarly plastic egg protection strategies if their eggs are vulnerable to attack by predators and if competition for nest sites drives the use of diverse nest microhabitats. These criteria probably apply to other birds, such as some boobies (Suliformes), pelicans (Pelecaniformes), and flamingos (Phoenicopteriformes), whose pale eggs appear to become stained in the nest (Schmidt 1958; del Hoyo et al. 1992) and which additionally experience competition for nesting habitat.

Finally, we note that the capacity to stain eggshells behaviorally could be enhanced by the microstructure of the eggshell. Blue-footed booby eggshells are chalky because they possess an outer layer of amorphous calcium carbonate called vaterite (Tullett 1984). Interestingly, Suliformes,

Pelecaniformes, and Phoenicopteriformes possess similarly chalky eggshells, and it is likely that this increases absorptivity and boosts adherence of nest material during behaviorally induced camouflage. Thus, we hypothesize that instead of using pigments to conceal their eggs, these lineages have instead exploited the ultrastructure of their shells to facilitate behaviorally induced camouflage, perhaps responding to selection for nesting in limited yet diverse exposed sites. It remains to be seen whether the vaterite layer evolved specifically to facilitate adaptive camouflage or for another purpose, such as microbial defense (Tullett et al. 1976), and was subsequently coopted for camouflage.

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