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Daizaburo Shizuka

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Extreme offspring ornamentation in American coots is favored by selection within families, not benefits to conspecific brood parasites

Bruce E. Lyon^{a,1} and Daizaburo Shizuka^b

^aDepartment of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060; and ^bSchool of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE 68588

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Offspring ornamentation typically occurs in taxa with parental care, suggesting that selection arising from social interactions between parents and offspring may underlie signal evolution. American coot babies are among the most ornamented offspring found in nature, sporting vividly orange-red natal plumage, a bright red beak, and other red parts around the face and pate. Previous plumage manipulation experiments showed that ornamented plumage is favored by strong parental choice for chicks with more extreme ornamentation but left unresolved the question as to why parents show the preference. Here we explore natural patterns of variation in coot chick plumage color, both within and between families, to understand the context of parental preference and to determine whose fitness interests are served by the ornamentation. Conspecific brood parasitism is common in coots and brood parasitic chicks could manipulate hosts by tapping into parental choice for ornamented chicks. However, counter to expectation, parasitic chicks were duller (less red) than nonparasitic chicks. This pattern is explained by color variation within families: Chick coloration increases with position in the egg-laying order, but parasitic eggs are usually the first eggs a female lays. Maternal effects influence chick coloration, but coot females do not use this mechanism to benefit the chicks they lay as parasites. However, within families, chick coloration predicts whether chicks become “favorites” when parents begin control over food distribution, implicating a role for the chick ornamentation in the parental life-history strategy, perhaps as a reliable signal of a chick’s size or age.

conspecific brood parasitism | offspring ornamentation | American coot | social selection | parental choice

Darwin turned his focus to ornamental traits because they seemed to defy the logic of his theory of natural selection: These traits could not be explained by ecological benefits like survival or foraging. His second important theory, sexual selection, proposed that ornamental traits are favored because they enhance the mating success of the bearers, either through mating preferences for ornaments or through intrasexual competition over mates (1). A wealth of studies has confirmed the ubiquity of sexual selection (2), so much so that ornaments are sometimes viewed exclusively in the context of sexual selection. However, over the past couple of decades we have come to realize that ornamental traits commonly occur in contexts other than mating, in particular social competition and offspring ornamentation (3–9).

Offspring ornamentation has been documented in a number of taxonomic groups [natal coats in mammals (10, 11), ornamental plumage in birds (12, 13), mouth color in birds (14), begging vocalizations and displays in birds and insects (15, 16)]. The key attribute shared by these taxa is parental care invested in offspring. Two complementary approaches have been used to investigate ornamental offspring traits, both of which relate to parental care. The first approach is analogous to the study of sexual selection via mate choice. West-Eberhard proposed that

competition within families can favor the evolution of offspring ornamentation (4). According to her parental choice theory, parental choice can lead to the evolution of offspring ornaments if parents preferentially invest limiting resources like food in the most ornamented offspring in the family (4). Parental choice is an evolutionary mechanism analogous to mate choice, except that the limiting resource is food, not matings, and the evolutionary response involves ornamental traits in offspring rather than breeding adults. Parental choice theory assumes that parents have a preference for ornamentation, but it makes no assumptions about why parents evolve the preference in the first place.

A second approach to understanding offspring ornaments is signaling theory, which considers the information, if any, that ornamental traits might contain and therefore why signal receivers would attend to the signal. The extensive literature on offspring begging or solicitation takes this approach (e.g., refs. 17–19). From its inception, the begging literature noted that the evolution of offspring signals occurs in the context of conflicts of interest within families over parental investment (17, 18, 20). A multitude of conflicts potentially exist within families, including parent–offspring conflict (21), sibling rivalry (22), and sexual conflict between parents (23). These conflicts are not mutually exclusive and Parker et al. (24) provide a framework that considers the interplay of all 3 conflicts simultaneously. These potential evolutionary conflicts force us to consider whose fitness stakes drive the evolution of offspring signals. Do begging and

Significance

Bright colors in animals are often used for courtship, but some animals are born with such ornaments, posing an evolutionary puzzle: What are juvenile ornaments for? We studied variation in color of bright juvenile ornaments of American coot chicks (orange/red feathers, beak, and head) to ask why they might have evolved. Coots lay eggs in each other’s nests, but brood parasitic chicks were less colorful than host chicks, suggesting ornaments are not used to dupe hosts into feeding them more. Instead, chicks from later eggs were redder, and redder chicks were more likely to be chosen as the favored chicks that parents pamper. Chick coloration allows parents to invest in the chicks that most benefit from parental food.

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¹To whom correspondence may be addressed. Email: belyon@ucsc.edu.

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other offspring ornamentation contain information that helps parents maximize their fitness by enabling them to optimize the quality and quantity of offspring produced (18)? Or does it coerce parents into providing more resources than the parental optimum (21)? Or, perhaps, begging is primarily driven by sibling competition (25). In some taxa, sibling competition and sexual conflict are increased by the occurrence of extrapair paternity, where some of the offspring are sired by a male other than the social mate (15). Although much of the field has focused on an honest signal basis to parental choice and offspring signals, it is important to realize that the traits and selection can result for purely social and sensory reasons (4).

In addition to intrafamilial conflict, offspring signals could also be shaped by conflicts between families. Such conflict can occur when offspring of different parentage occur in a given nest, for example due to brood parasitism. Brood parasitism, i.e., laying eggs in the nests of others, occurs both between and within species, and both forms can affect the evolution of offspring signals. Offspring of interspecific brood parasites often evolve elaborate begging strategies to increase provisioning rates by the host parents (26), often by mimicking host offspring to tap into existing parent–offspring communication systems (27). Parasitism within species is also common in birds (28) and results in nests containing offspring from multiple females (and multiple males) that may compete for parental resources. In this case, there is scope for both intrafamilial conflict (e.g., parent–offspring conflict, sibling rivalry, and sexual conflict) as well as interfamilial conflict (e.g., offspring from different females) in driving offspring signals. Kilner (14) discussed the potential role of all of these different conflicts in the evolution of 1 particular form of offspring ornamentation, mouth coloration in avian chicks.

In this study, we use a case of extreme juvenile ornamentation in American coots (*Fulica americana*) to investigate the scope for intra- vs. interfamilial conflict as a driver of chick coloration. American coots are rails (Rallidae), a family containing some of the most extremely ornamented offspring found in nature (12, 13, 29). Newly hatched American coot chicks have a combination of colorful plumage, highly modified feathers, and bare patches of colorful skin (Fig. 1A). In an early test of parental choice theory, Lyon et al. (12) manipulated the plumage color of half the chicks in experimental broods and showed that parents preferred the more ornamented offspring. Ornamented offspring received more food, grew faster, and had higher survival than unornamented offspring. The study confirmed the existence of parental choice as an evolutionary mechanism that can favor offspring ornaments. However, the question remains as to why coot parents show the preference in the first place. As with mate-choice studies, showing that choice exists is fairly straightforward, but showing why the choice exists is much more difficult (2, 30). In particular, a key question is: Whose fitness interests are served by the parental choice, and how? Does choice for particular offspring traits reflect an adaptive parental behavior that benefits the parents' fitness, or might some players be exploiting sensory aspects of parental preference for their own benefit, perhaps at the detriment of the parents' fitness (31, 32)?

In addition to preferring ornamented offspring, coots exhibit parental preference among offspring based on 2 other criteria: Parentage and hatching order. Coots are prolific conspecific brood parasites; about 40% of nests contain at least 1 brood parasitic egg (33). Most parasites are nesting females who are both brood parasites and parents, and these nesting parasites are also sometimes hosts that raise the offspring of other brood parasites (33). Shizuka and Lyon showed that coots learn to discriminate between host and parasite chicks with an imprinting-like mechanism based on the set of chicks that hatch first in a given nest, and the parents then reduce the survival of parasitic chicks primarily by direct infanticide (34). In a separate study, Shizuka and Lyon examined preferential provisioning based on hatching order within the nest

(35). Coot eggs in a nest hatch asynchronously, with an average of 9 to 10 eggs hatching over a period between 2 and 11 d, depending on the nest (median 6 d). After an initial stage of scramble competition among offspring during which most chick mortality takes place, parents switch to preferentially provisioning of the youngest (i.e., later-hatched) still-surviving chicks during the later stages of parental care, a pattern of favoritism enforced by aggression toward older (earlier-hatched) chicks (35). In addition, each parent specializes on their own favorite chick (35).

Here we build on these previous studies of parental choice by examining correlates and consequences of natural patterns of chick plumage variation in American coots. Studying the same populations studied in our previous work, we addressed the following questions. First, is chick ornamentation selectively favored through fitness gained within families or between families via brood parasitism? Brood parasitism could explain chick ornamentation if parasitic chicks are consistently more ornamented than nonparasitic chicks. We found the opposite—parasitic chicks were duller than nonparasitic chicks—so we then turned our attention to patterns within families to examine which aspects of intrafamilial dynamics might drive juvenile ornament evolution. Because almost all aspects of parental care and offspring survival in coots are connected to an egg's (and chick's) position in the hatching order, our second question was whether ornamentation varies with laying/hatching order. Third, we asked whether within-brood variation in juvenile coloration affects the pattern of parental preference during the later phase of parental care when parents show extreme favoritism. Finally, we determined whether natural levels of variation in ornamentation matter to chick fitness in terms of their survival. We examined the relation between survival and ornamentation in 2 ways: 1) Observationally, based on natural variation within and between broods; and 2) experimentally, with a cross foster experiment that increased the range of variation within broods while simultaneously dampening the effects of hatching asynchrony on chick survival.

Results

Trait Variation and Correlations. We measured correlations between different color traits from 1,431 chicks. Correlations between the different coot chick color traits were variable (Fig. 1B and *SI Appendix*, Fig. S1). In general, dynamic color traits, such as shield and pate coloration, were not strongly correlated with static color traits, such as beak, papillae, and chin plumage. Additionally, the 2 dynamic traits showed low correlations with each other. Because we were primarily interested in understanding causes and consequences of variation in static colors, we conducted a principle components analysis (PCA) to summarize 9 static color measures (red chroma, hue, and brightness for each of the 3 static traits: beak, papillae, and chin feathers). The first 3 principle components (PC) axes had eigenvalues greater than 1, and cumulatively explained 64% of the variance in static color measures. The first PC axis (PC1) alone explained 34% of the overall variance in static color. This PC axis generally captured the “redness” of the chick, with positive loadings for chroma and hue values and negative loadings for brightness values across all 3 static traits (*SI Appendix*, Table S1).

Chick color traits varied among the broods of different females: Among brood variation was significant for all but 1 of the color traits, and in all of the first 3 PC axes summarizing static color measures (Table 1). *P* values in Table 1 are adjusted to control for false-discovery rate (36). The PC1 measure of color showed the strongest pattern of between-female variation and, among the individual trait measures, chroma values of chin plumage showed the greatest among-female effect (Table 1). Clutch size and average egg size did not have an effect on the average chick color for a given female (clutch size: $F = 0.49$, $P = 0.49$; average egg size: $F = 1.19$, $P = 0.28$). There was a relatively weak negative effect of laying date of the first egg on chick redness

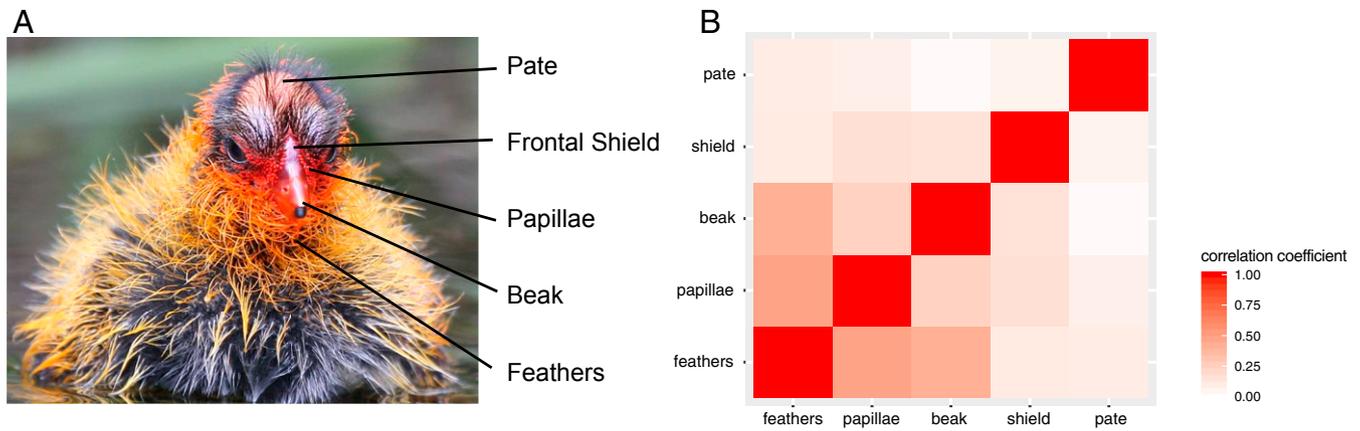


Fig. 1. Chick color traits and their correlations with each other. (A) The 5 traits measured include pate, frontal shield, beak, papillae, and plumage. (B) Visualization of the correlation matrix of red chroma measurements from each of the 5 traits. The color of each trait is the average of at least 3 measurements per trait per individual. Colors represent correlation coefficients.

($F = 4.73$, $P = 0.03$) and a stronger effect of reneating on chick color: Chicks in nests that were reneating attempts by a breeding pair were redder than those from first nesting attempts (Fig. 2) ($F = 9.04$, $P = 0.003$).

Chick Coloration and Hatching Order. We assessed the relationship between hatching order and chick color for all chicks, excluding parasitic chicks. Chick color shows a strong relation with hatching order. Later hatched chicks have higher PC1 values: That is, they are redder and darker than early-hatched chicks (Fig. 3) ($n = 1,377$ chicks from 305 nests, $F = 115.9$, $P < 0.0001$). We also conducted the analysis using 558 chicks for which we knew the exact laying sequence (as opposed to hatching day), and the result was the same (SI Appendix, Fig. S2) ($F = 67.0$, $P < 0.001$).

Parasitic Chicks Are Less Red than Host Chicks. We determined if parasitic chicks are redder than nonparasitic chicks generally (i.e., both host chicks and chicks in nonparasitized nests). Contrary to predictions from the parasite benefit hypothesis, parasitic chicks were less red than nonparasitic chicks (ANOVA on color PC1, $n = 1,377$ host chicks and 54 parasite chicks from 310 clutches; $F = 5.6$, $P = 0.019$). Restricting the comparison to naturally parasitized nests and running a mixed-effects model with nest as a random effect revealed a similar pattern for overall color (Fig. 4) (color PC1: $n = 124$ host chicks and 54 parasite chicks from 27 nests; $F = 5.9$, $P = 0.015$). The overall difference between parasites and hosts is even more apparent once we account for hatching order in the host nest (Fig. 4) ($n = 124$ host chicks and 54 parasite chicks from 27 nests; host/parasite: $F = 13.9$, $P < 0.001$; hatch order: $F = 16.7$, $P < 0.001$). Note that host chicks show increasing redness with hatching order, but this pattern is less apparent among parasitic chicks.

Effect of Chick Color on Parental Favoritism. We asked if patterns of parental favoritism are based on chick color in unmanipulated broods. About 10 d after the last chick hatches, parent coots exhibit extreme favoritism where each parent chooses a different favorite chick to feed heavily and, in most broods, the favored chicks are among the youngest (i.e., last-hatched) of the chicks that survive to fledging (35). We therefore determined whether chick color correlates with this favoritism status (favored by male, favored by female, or not favored by either). We found that color influences the probability that a chick is favored by a parent: Redder chicks were more likely to be favored by 1 of the 2 parents (Fig. 5) (generalized linear mixed model [GLMM] with nest as random effect, likelihood ratio test: $\chi^2 = 7.3$, $R^2 = 0.07$,

$P = 0.007$). There was no statistical difference between the redness of the favorites of female and male parents (ANOVA: $F = 1.78$, $P = 0.19$).

In contrast to the patterns seen in unmanipulated broods, we did not find any effect of chick color on probability of being favored in experimental synchrony broods (GLMM: $\chi^2 = 0.27$, $R^2 = 0.005$, $P = 0.60$).

Chick Coloration and Survival.

Within-brood variation in chick color has limited effect on survival. We assessed the relation between color and survival for 332 nonparasitic chicks in 53 unmanipulated broods. We excluded parasitic chicks in this analysis because previous experimental results show that coots can reject parasitic chicks during the period of parental care (34). We found no effect of chick coloration on chick survival independent of hatching order. With a mixed-effects Cox model using color PC1 (relative to brood mean) as a measure of chick color, hatching order affected survival but not chick color (hatch order, $z = 3.38$, $P < 0.001$; color PC1, $z = -0.32$, $P = 0.75$).

We also assessed the relation between color and survival for 168 chicks in 22 experimental synchrony broods. This experiment controls for the effects of hatching order on chick survival.

Table 1. Results of ANOVA analyses of across-brood variation in chick color traits (i.e., separate model for each color trait)

Trait	F	P
Chin plumage brightness	2.76	<0.001
Chin plumage chroma	4.36	<0.001
Chin plumage hue	4.01	<0.001
Papillae brightness	2.02	<0.001
Papillae chroma	2.28	<0.001
Papillae hue	2.71	<0.001
Beak brightness	2.16	<0.001
Beak chroma	2.50	<0.001
Beak hue	2.08	<0.001
Shield brightness	1.24	0.009
Shield chroma	1.55	<0.001
Shield hue	1.37	<0.001
Pate brightness	1.90	<0.001
Pate chroma	3.17	<0.001
Pate hue	0.79	0.99
PC1	5.03	<0.001
PC2	2.52	<0.001

P values are adjusted to control for false-discovery rate (36).

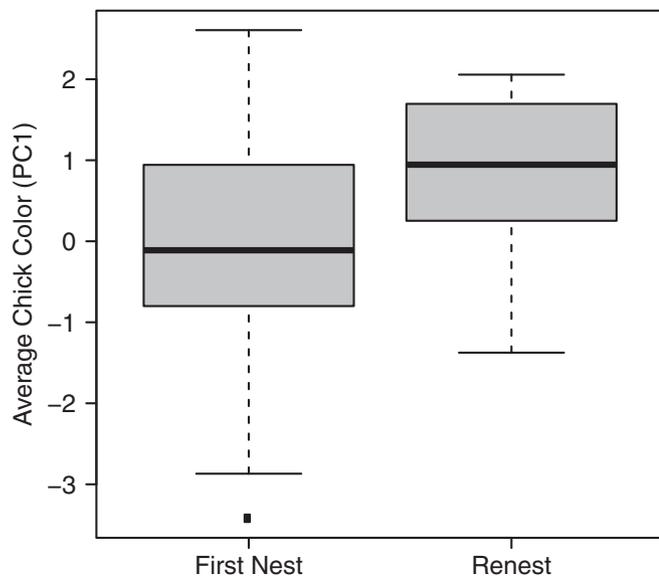


Fig. 2. Chicks are redder on average in renests that following the failure of an initial nest of a female compared to chicks in successful first nesting attempts.

We found no relation between redness (color PC1, measured relative to the brood mean value) and chick survival ($\chi^2 = 2.27$, $P = 0.13$).

Discussion

Correlates of Variation in Chick Coloration. Our analyses show that there is substantial variation in chick coloration within and across broods. Within broods, there is a clear and strong effect of laying sequence and hatching order on chick color; chick redness increases with hatching order, which reflects laying order. The correlation between hatching (and laying) order and chick color strongly implicates maternal effects as a determinant of within-brood variation in chick color because chicks cannot control the order in which their egg is laid and hatched. There is ample evidence that egg size and egg yolk content vary with laying order in many birds (37, 38). For American coots specifically, Reed and Vleck (39) showed that egg androgen content declines with laying order. Egg size also varies with laying sequence in American coots; the first eggs are typically relatively small, eggs 2 to 5 are the largest, then size declines again for later-laid eggs (40, 41). American coot eggs are known to contain very high amounts of carotenoids in the yolk (42), the highest yet reported for birds, and it is likely that carotenoid content of eggs varies among females and with laying sequence for a female, producing both among- and within-brood variation in chick color. In terms of known effects on chick survival, it is interesting that the relation between egg-laying order and egg androgens is in the opposite direction to the pattern we detected for chick coloration. This might suggest that the underlying mechanisms that connect these different attributes to chick fitness are somewhat independent or have opposing effects.

Chick Ornamentation Is Not Favored through Fitness Females Gain from Brood Parasitism. A key finding of our study is that potential fitness benefits from brood parasitism is unlikely to explain the extraordinary offspring ornaments in newly hatched American coot chicks, at least in terms of current patterns of variation and selection. Parasitic chicks were less ornamented than nonparasitic chicks, a pattern that held both for comparisons with all nonparasitic offspring in the population and for comparisons restricted with host chicks at parasitized nests. Our previous work

showed that parent coots show a strong relative preference for ornamented chicks over experimentally unornamented chicks in their brood (12), so chick ornamentation would only benefit brood parasites if parasitic chicks tended to be more colorful than nonparasitic chicks.

In American coots, parasitic females are not a distinct category of females; instead, most females gain some of their fitness from parasitism and some fitness from typical nesting. It is important to consider that fitness from ornamented chicks could affect more than 1 component of fitness for a given female, and that there may be trade-offs between the fitness from these different components. In our population, most parasitism is by females that also have nests of their own; these females lay their parasitic eggs first and follow with eggs laid in their own nest (33). These nesting parasites could produce more ornamented parasitic chicks in 2 ways. First, parasitic females could be higher-quality females that consistently produce more ornamented offspring generally, both parasitic and in their own nest. Parasites do tend to be older females that lay more total eggs (43), so female quality could provide a feasible mechanism. Second, females could strategically invest in eggs that are destined to be laid parasitically. The observation that parasite chicks are less ornamented than nonparasitic chicks, however, rejects both of these possibilities.

Why don't female coots make parasitic chicks that are more ornamented, thus increasing the possibility that they would be favored in the host nest? We suggest that laying order effects may preclude strategic investment in eggs destined to be parasitic; within broods, chick ornamentation increases with position in the laying order. Lyon (33) showed that at least 67% of parasitic eggs were laid by females with their own nests (i.e., not floaters), and most (84%) of the parasitic eggs laid by those nesting females were laid before they laid their own clutches in their own nests. Looking in more detail at the specific position in the laying order for the 217 of these parasitic eggs for which we had exact order in the female's laying sequence, 58% of the parasitic eggs were among the first 3 eggs laid by the female, while 69% were among the first 4 eggs laid by these females.

The chicks from parasitic eggs may be less ornamented simply because they are from the first eggs the female lays in the season. One possibility is that the laying order relation with chick color is a physiological constraint that is difficult to break. Alternatively, it may also be that females cannot predict sufficiently in advance that they will have the opportunity to be parasitic and adjust their

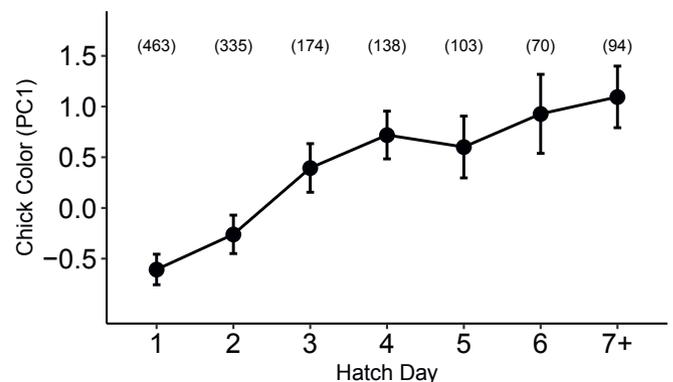


Fig. 3. The relationship between hatching order and chick redness (color PC1). Dots represent mean chick color (PC1) across all individuals for a given position in the hatching order. Lines are 95% CI ($1.96 \times SE$). Hatching order is day of hatching and more than 1 chick in a brood can have the same hatching day. We pooled the data for chicks hatching on day 7 and later. The numbers in parentheses indicate the sample size of chicks at that position in the hatching order.

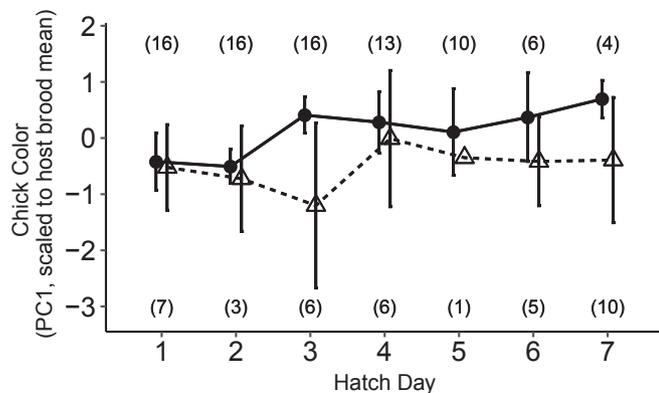


Fig. 4. Color of host (filled circle, solid line) and parasite chicks (open triangle, dotted line) across hatching order in naturally parasitized nests. Hatching order is day of hatching and more than 1 chick in a brood can have the same hatching day. Due to reduced sample size of chicks later in the hatching sequence, we pooled the data for chicks hatching on day 7 and later. The y axis is scaled relative to the average host chick color. Lines are 95% CI ($1.96 \times SE$). The numbers in parentheses are sample size of host chicks (above) and parasite chicks (below) at each position in the hatching order.

egg contents accordingly. Parasitism appears to be opportunistic: Most parasitism involves immediate neighbors and a female can only lay parasitically if she has neighbors with eggs when she is ready to lay because evidence suggests that females do not wait for hosts to become available (43). This opportunism, coupled with the fact that coot eggs take 7 d to form (44), suggests that females might not be able to reliably invest strategically in eggs that end up being laid parasitically because they cannot predict sufficiently in advance whether they will have the opportunity to lay eggs parasitically.

Chick Coloration and Conflicts within Families. If fitness from parasitism is unlikely to explain coot chick coloration, then any selective benefit to variation in chick ornamentation should be due to selection within families. Such selection could occur for several reasons, some involving conflicts of interest, others cooperation. Our findings suggest that 2 conflicts of interest are unlikely as drivers of chick coloration, but we note that definitive tests are very difficult. The evolution of chick ornamentation could involve parent–offspring conflict (21); chick ornamentation might allow chicks to extract more parental care than is the parents’ interest. Our findings reject this idea because variation within families correlates with position in the egg-laying order, an indication that maternal effects account the within-family variation. However, it is possible that this maternal control represents the outcome of the resolution of past parent–offspring conflict-driven battles (14).

Maternal control of variation within broods is, however, consistent with a second evolutionary conflict, sexual conflict between the parents. Müller et al. (45) suggest that females could use maternal hormones to produce offspring traits that cause the male to increase investment in offspring, and the same logic could apply to other maternal effects generally, including color of eggs or offspring (46, 47). In addition, hatching patterns and hatching order effects like those we observed in coots have also been implicated in sexual conflict: For example, Slagsvold and Lifjeld (23) proposed that different hatching patterns could influence the relative parental investment and costs of the sexes differently, and hence that hatching patterns could drive sexual conflict. In American coots, egg hormones, chick ornamentation, parental feeding rates, and offspring survival all correlate with an egg’s position in the laying order, consistent with the hypothesis that maternal effects or hatching patterns could be driven by

sexual conflict. Experimental manipulation of both plumage and hatching patterns are needed to rigorously test the sexual conflict hypothesis. Nonetheless, the present finding—that chick coloration correlates with parental favoritism and investment patterns equally in both sexes—suggests that chick coloration patterns are more likely to reflect tactics that involve parental cooperation than sexual conflict.

Chick Redness Affects Parental Favoritism but Does Not Directly Affect Survival. A key result of our study was the discovery that variation in chick coloration correlates with parental favoritism in broods with natural hatching patterns. This is an important finding because it suggests that chick coloration—and parental preference for colorful chicks—represents a parental strategy that is adaptive for both parents and is not driven by sexual conflict. Although the female parents control the relation between chick color and egg sequence, a mechanism that could potentially manipulate males into increasing their parental investment, the fact that both parents follow same general pattern of favoritism in terms of relative hatching order (35) and color (present study) suggests that any relation between chick coloration and favoritism benefits both parents.

Some context is necessary to fully appreciate the links between chick coloration, hatching asynchrony, and parental favoritism. Brood reduction is extreme in American coots: On average, parents lose about 50% of their chicks before independence due to starvation, and it is primarily the later-hatching chicks that starve (33, 35). Most chick mortality occurs early after hatching (first 10 d) when parents do not control food allocation but instead feed the first chick that reaches them when the parent finds a prey item. The older chicks get more food, and therefore survive better, because their large size allows them to swim faster and get to parents first. However, starting at about 10 d after the last chick hatches, parents begin to control food allocation and reverse the competitive advantage of the older chicks. Parents use selective aggression toward the older chicks to ensure that the youngest (i.e., latest-hatching) of the remaining chicks get the most food (35). Each parent chooses a single “favorite” chick that receives about 80% of feeds from that parent but receives almost no feedings from the other parent. Most (65%) of these favored chicks were among the last-hatching chicks among the surviving chicks (i.e., chicks surviving to the end of the observation period).

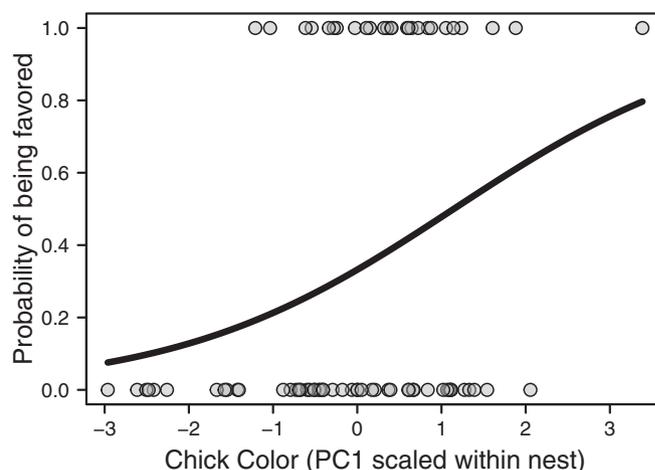


Fig. 5. The probability that a chick becomes a parental favorite increases with color. Line is predicted fit based on general linear model with binomial error. See text for statistical results using generalized linear mixed model.

We now add to the previous work on parental favoritism by showing that favorite chicks not only are later-hatched chicks, but they are also more colorful. However, because both chick color and favoritism correlate with hatching position, observations from natural broods alone do not provide convincing evidence that parents are using chick color per se to decide which chicks to feed; some other correlate of hatching order, like chick size, could explain the observed pattern. However, the combined results from our 2 experiments that separately modified chick coloration and hatching asynchrony (ref. 12 and the present study, respectively) together provide convincing evidence that parents are using the color itself, but that hatching position is also important in when parents pay attention to chick color. By experimentally altering chick coloration in the previous study (12), we showed that plumage coloration itself dramatically affects parental feeding decisions, but there was also an interaction with hatching order whereby colorful plumage only benefits later-hatched chicks. In the present study, when we experimentally reduced hatching asynchrony we found that natural levels of variation in chick coloration did not predict which chicks became parental favorites, in striking contrast to the broods with natural levels of asynchrony. Thus, parents use chick color to choose favorites, but only do so when hatching is asynchronous.

Why would parents use chick color to make their decisions about favoritism? One possibility is that color serves as a reliable signal of the chick's size or age, particularly at the point when parents begin to favor a single chick (12). If this were the case, the relative color of juvenile ornamental may serve as a signal that helps the parent invest parental care in a manner that maximizes both the fitness of the favored offspring and the parent (18, 19). Chick color could provide an honest signal of size or age in 2 ways. First, the strong correlation between color (redness) and egg sequence/hatching day could be used as a cue for relative age of chicks. Second, the color of ornaments may change with increasing chick size due to fading or the decrease in relative density of ornamental plumage with increasing surface area of chicks. In unmanipulated broods, these 2 effects would reinforce each other. In contrast, in our experimental synchrony broods, the color of chicks would be decoupled from the egg sequence and hatching order, but it is yet unknown whether the timing of fading of ornamental traits was correlated with chick size in these broods. Thus, our results suggest that the former mechanism (egg sequence effect) may be sufficient as an honest signal of relative age, although the latter effect (fading/dilution effect) could be an additional, reinforcing mechanism.

The likelihood that chick color eventually changes with age or size, through dilution or fading of the color, raises the issue of the temporal mismatch between when we obtained our color measurement (at hatch) and when parents exert parental control and show completely parental favoritism (around day 10). If chick color changes quickly with age, and if change is sufficiently uncorrelated with hatch color, then our measurement might not be useful for investigating links between chick color and parental favoritism. However, were this to be the case, we should not have found a clear association between color measured at hatch and the likelihood that a chick becomes a parental favorite because random changes in color would obscure rather than produce this clear pattern. This suggests that either hatch color correlates with color when parents exert control and choose their favored chicks (i.e., after day 10), or alternatively, that chick color at hatching begins to bias parental provisioning toward redder chicks in earlier stages but the patterns become more observable during the period of parental favoritism.

Although chick coloration correlates with parental favoritism, we were unable to detect a clear relation between chick coloration and survival in either unmanipulated broods or the mixed synchrony experiments that controlled for the effects of hatching asynchrony. For the unmanipulated broods, the lack of pattern

may result because by the time parental favoritism is established, the period of heavy chick mortality has already occurred, and that mortality is almost entirely determined by a chick's position in the hatching order (34). Moreover, parental favoritism functions to level the playing field for the disadvantaged late-hatched chicks; their increased feeding rate enables them to catch up with their earlier siblings in terms of growth (34). As such, enhanced ornamentation should reduce the mortality rate of these chicks relative to what it would be without the parental favoritism, and experiments may be required to detect survival effects. We have now done 2 such experiments. Our synchrony experiments, which manipulated hatch pattern but not chick coloration, did not yield clear survival patterns. However, when the color variation among chicks was drastically magnified while leaving hatching asynchronous—as in our earlier experimental study where orange plumes were trimmed from half of the chicks in each brood—striking survival patterns did emerge (12). Even in that experiment, however, hatching order still played a role and the plumage experiments only affected the survival of later-hatched chicks in the brood (12). Taken together, all of these observations indicate that the interaction between offspring coloration and parental preference in American coots is strongly dependent on the order in which eggs are produced and hatched within a clutch. Overall, the various patterns we found suggest that extant patterns of variation in chick color make sense in terms of parental care strategies that benefit both the parent and the ornamented offspring.

Conclusions. We have shown that the current patterns of variation in chick coloration correlate with a parental strategy to optimize food allocation within families: Hatching asynchrony, followed by brood division and parental favoritism of the smallest most colorful chicks that remain after a period of scramble competition and brood reduction (35). However, these patterns do not necessarily explain why American coot chicks show such extreme ornamentation compared to many other close relatives (13). One or more other factors could have feasibly contributed to the evolutionary elaboration of juvenile ornaments. For example, we studied only a subset of the many ornaments that coot chicks have, that include both static and dynamic signals, and it seems unlikely that each of these different ornaments evolved completely independently of each other. Selection for parents to attend to some ornaments could have favored the evolution of parental preference patterns that then set the stage for other ornaments that mimic or amplify the original trait that selects for parental preference (32). Second, Kilner (14) suggested that current patterns of variation in chick signals may reflect the resolution of past evolutionary conflicts within families. In the case of American coot chicks, current levels of ornamentation could reflect the resolution of conflicts both within and between families (i.e., conspecific brood parasitism). Finally, these factors could work in conjunction with purely social factors, whereby factors that initially favor parental preference potential create the conditions for runaway social selection that would exaggerate the trait well beyond levels favored parental preference in the first place (4, 48). One way to resolve these outstanding questions would be to leverage the natural variation in juvenile ornamentation within this family of birds [Rallidae (13)] to conduct comparative studies of the relation between chick coloration, parental favoritism, and brood parasitism.

Methods

Study Area and Species. We studied American coots at 5 different wetlands in central British Columbia, Canada from 2005 to 2008: 3 wetlands that comprise the Westwick Lakes near Williams Lake, Pond 42 (49) at Beecher's Prairie near Riske Creek, and Jaimeson Meadow near Big Creek. At these wetlands, coots defend territories that contain patches of hardstem bulrush (*Schoenoplectus acutus*) in which they nest. Bulrush is the dominant emergent plant at all

wetlands and was limited to a shoreline strip on most wetlands, but sparse patches grew in the middle of Jaimeson Meadow, providing nesting cover for coots away from the shoreline.

Coots breed in pairs and both sexes participate in all aspects of parental care: Territory defense, nest-building, incubation, and feeding the chicks. Clutch size is relatively large but variable (median = 9 eggs, range 4 to 15 eggs, $n = 279$ clutches). Nests are built in vegetation over water and incubation begins well before clutch completion (50), which results in a pronounced hatching asynchrony (33, 35). Coot chicks leave the nest soon after hatching but require parental food for at least 10 d, at which point they can begin to feed themselves; some chicks are fed for 30 to 40 d (33, 35). Overt sibling aggression does not occur, but chicks compete for parental food by following parents during foraging forays, which always occur within the breeding territory. Death by starvation is common, mostly in the first 10 d when there is no direct parental control of food allocation; in broods that successfully hatched chicks, half of the offspring died before independence (51% of 601 eggs produced independent young). Most broods fail to fledge all of the chicks that hatch (93% of 61 nests), and chicks hatching later in the sequence have disproportionately high rates of mortality (33, 35).

Monitoring Nests and Detecting Brood Parasitism. Most nests were found very early in the laying stage and were then monitored every 1 to 4 d during egg-laying. On each visit, all new eggs were given a unique number with a permanent marker. Individual females can only lay 1 egg per day so we detected parasitism by the appearance of more than 1 egg per day (e.g. refs. 33, 51, and 52). Once parasitism was detected at a nest we visually compared among eggs to determine which eggs were laid by brood parasites (33). For some of these eggs, we were also able to make comparisons among nests and determine which females in the population laid the eggs: This was possible for parasites that also had their own nests (33). The accuracy of these methods has previously been verified for American coots with discriminant function analysis using egg features (53) and DNA fingerprinting (54). McRae and Burke (55) found a perfect correspondence between field and genetic methods for determining parasitism in the common moorhen (*Gallinula chloropus*). During our study (2005 to 2008), 54 nests were parasitized, and at least 1 parasitic chick hatched in 27 nests.

Determining the Position in the Egg-Laying Order for Parasitic Eggs. The position of an egg in a female's laying order turns out to be important for patterns of chick color variation, for both parasitic and nonparasitic eggs. For parasitic eggs, in the present study we did not follow parasitic nests closely enough to be able to determine the exact egg-laying order of the parasitic chicks whose color we measured. However, we do have this resolution of information for a subset ($n = 217$) of the parasitic eggs followed in a previous study (53), and we use those data here to estimate the percentage of parasitic eggs laid by parasitic females that were within their first 3 laid eggs and first 4 laid eggs in a season, respectively.

Hatching Chicks in Captivity. We hatched chicks in captivity to ensure that all chicks could be captured: The precocial chicks can leave the nest within hours of hatching and thereafter be almost impossible to capture. Hatching chicks in captivity also made it easy to match chicks to their respective eggs at each nest, and to obtain color measurement for a large number of chicks. Nests that approached their expected hatch date were checked daily. We took eggs from nests at the first sign of pipping, typically 1 or 2 d before the chicks hatched. Each egg was uniquely labeled (by egg number and nest), placed its own sealed individual mesh pouch with a paper label with nest and egg ID, and hatched in an incubator (Hovabator model 1602N, GQF Manufacturing). Each chick received a color-coded nape tag that was individually unique within its brood so we could follow individual chicks throughout the parental care period (56). We returned chicks to nests within 24 h of hatching. Because of pronounced hatching asynchrony, nests were never left with fewer than 2 eggs or chicks, and parents did not abandon the nest during this period (34, 35).

Cross-Fostering Experiment to Create Synchronously Hatching Broods. A cross-fostering experiment we designed to assess parasitic chick recognition (34) can also be informative for investigating whether natural levels of color variation affect chick survival. From 2005 to 2007, 30 nests were set up as "mixed synchrony" nests, in which host chicks were matched with a roughly equal number of foreign chicks on the first day or first 2 d of hatching, depending on hatching patterns (we matched brood size to clutch size). We now know that hosts learn which chicks are likely to be their own by imprinting on the first chicks that hatch (34). In the mixed-synchrony broods parents would have learned that both their own chicks and the foreign

chicks in their brood were their own and should not have been able to distinguish their own from the foreign chicks, a prediction that was borne out by chick survival data (ref. 34 and reconfirmed here) (effect of host vs. foreign chick on survival, mixed-effects Cox model: $z = -1.21$, $P = 0.23$). The mixed-synchrony experiments allow us to now examine whether natural levels of chick coloration correlate with fitness by altering hatching asynchrony, an important factor that influences the potential effect of chick coloration. By reducing the degree of hatching asynchrony, and its pervasive influence on chick survival, we might increase the potential for chick coloration to affect chick survival.

Monitoring Broods for Survival of Individual Chicks. We conducted censuses and feeding observations periodically throughout the parental care period (median = 9 observations per brood; median last day of observation = 25 d after hatching completion). Brood censuses and behavioral observations were conducted at close range (10 to 40 m) from floating mobile blinds equipped with camouflage coverings.

For feeding observations, we typically followed 1 parent for focal observations up to 30 min, and we supplemented these observations with opportunistic observations of feedings (e.g., when we could observe feedings from adjacent territories). Following a single parent to assess feeding rates per chick is feasible because coots show brood division, whereby the parents specialize on feeding completely distinct subsets of the brood, and the same division is maintained until the chicks are independent of parental feedings (35).

Measuring Chick Color Ornaments at Hatching. We measured the color of coot chicks ($n = 1,431$ chicks from 310 nests) soon after their plumage was dry but within 24 h of hatching. Chick color was measured prior to assignment to any subsequent experimental treatment. Color was measured with an Ocean Optics USB2000 spectrometer and a PX-2 pulsed xenon light-source; we measured a 2-mm diameter area of plumage at a 45° angle (57). We took several measures of each of 5 specific colorful body parts (Fig. 1A): Pate (4×), feathers around the chin and neck (6×; hereafter "chin plumage"), beak (4×), frontal shield (3×), and facial papillae (modified feathers; 4×), for a total of 21 measurements per chick. Our brood observations during this study revealed that pate color is a dynamic trait that can change rapidly over time. Beak color seems not to change rapidly over time and we are unsure about the degree to which the frontal shield changes color over time. We measured wavelengths from 300 to 700 nm and then converted raw measurements to 3 tristimulus variables: Total brightness (total area under the curve), red chroma (proportion of total brightness within 600 to 700 nm), and red hue (nanometers of the steepest increase in reflectance). We then calculated the average value of each of these 3 measures for each body part.

Because we have many correlated trait measurements, we used PCA to reduce our data for some statistical analyses. Based on our results showing that dynamic color traits (pate and shield color) and static color traits (beak, papillae, and chin plumage) are not tightly correlated, we focused our analyses on static colors. We did this, in part, to focus on fixed traits that permit an accurate measurement that does not depend on the social or physiological context. Thus, we conducted PCA for the 9 axes of static color (chroma, hue, and brightness for the 3 static traits). We used the `prcomp()` function in R v3.5.0 to use a singular value decomposition based on scaled and centered values.

Analyzing the Patterns of Chick Color Variation. We analyzed patterns of variation in chick color at hatching between broods as well as within broods. We first used ANOVA to compare variation in each aspect of chick color (each measure as well as first 3 PC axes) between adult females (i.e., broods; $n = 1,377$ nonparasitic chicks from 305 broods). In a second analysis we examined potential sources of among-brood variation in chick color using linear mixed models. For this analysis, we included 139 broods for which we had accurate data on egg sizes and date of first egg, and at least 5 chicks had been measured for color PC1 to reduce the potential effects of sampling error. For each brood, we calculated the mean PC1 score of chicks, excluding known parasitic chicks. We used these brood-average color scores (i.e., 1 point-measure of color per nest, indicating the average color of a chick produced by a female) as the response variable. The fixed-effect variables were clutch size (host eggs only), average egg size, laying date of the first egg, and whether or not the brood was a known re-nesting attempt by a breeding pair. We used wetland nested within a year as the random effect. For this and all subsequent linear mixed models, we fit the models using the "lme4" package (58) and generated P values using type III ANOVA with Satterthwaite approximation using the `lmerTest` package (59).

We used linear mixed models to determine whether within-brood variation in chick coloration was correlated with position in the hatching order ($n = 1,377$ chicks for which we had information on hatching order). We included brood as the random effect, hatch order as the fixed effect, and chick color (PC1) as the response variable. A chick's position in the hatching sequence (hereafter "hatch order") was based on the day it hatched relative to all others in the nest (hatch order of chicks hatched on first day = 1). When multiple chicks hatched on the same day at the same nest, they were classified with the same hatch order. Chick hatching order is very strongly correlated with egg-laying order (50), so we are ultimately assessing patterns that reflect changes in maternal investment with egg-laying order. We also repeated the analysis with 558 chicks that came from 98 nests that we found within the first 2 d of egg-laying and were checked daily throughout the laying stage. Thus, for these chicks we had exact information on egg-laying sequence except when nests were initially found with 2 eggs (in which case both eggs were assigned an egg sequence score of 1.5). We excluded parasitic chicks from this analysis because maternal effects would come from their mother and their egg's position in the parasite's laying order, not position in the host's laying order.

We used several approaches to explore whether color of parasitic and nonparasitic chicks varied systematically (focus on natural parasitism, not our experimental mixed broods with experimental parasites). First, we used simple ANOVA to compare the color of parasitic and nonparasitic chicks at the level of the population ($n = 1,377$ host chicks and 54 known parasite chicks). We then restricted analyses to parasitized nests ($n = 27$ nests containing 124 host chicks and 54 parasite chicks total). To ask whether host and parasite chicks differed in color within each parasitized brood, we used a linear mixed model with chick color (PC1) as the response variable, host/parasite status as the fixed effect, and brood as the random effect. Finally, we further asked whether parasitic chicks differed in color from host chicks given their position in the hatching order by using a linear mixed model with chick color (PC1) as the response variable, host/parasite status and hatching order as fixed effects, and brood as the random effect.

Assessing Whether Color Affects Parental Favoritism in Provisioning. We assessed whether chick color influenced parental allocation of food to chicks in unmanipulated broods. Previous work showed that the parental strategy for allocating food to chicks shifts dramatically between the early and late parental care periods (35). About 10 d after hatching is complete at a nest, each parent chooses a single "favorite" chick to which they devote about 80% of their feedings. This greatly influences the growth rate and survival of the youngest chicks that remain after the initial period of brood reduction. Based on these previous results, we assessed how chick color related to the

favoritism status of chicks during days 11 to 25 after hatching completion. Each chick was assigned to a favoritism category based on observed feeding patterns: That is, "favored by male," "favored by female," or "not favored." To ask whether ornamental color influenced whether or not a chick was favored by either parent, we conducted a GLMM with binomial error. The response variable was whether or not a chick was favored by either parent, the fixed effect was chick color (PC1, standardized within a brood), and brood was the random effect. We assessed the effect of chick color using a likelihood ratio test and estimated R^2 for the color effect using the package "r2glmm" (60).

We measured chick coloration at hatch but then assessed parental favoritism from days 11 to 25, raising the question of whether ornamentation at hatch is relevant to parental favoritism. In our previous study (35) we examined favoritism in smaller 5-d increments and found that favoritism patterns were already fully and strongly established by days 11 to 15 and did not change after that point. Since the pattern of parental favoritism does not change once it has been established, we are able to use the entire period of days 11 to 25 to increase sample size of observations in the present study. Therefore, it is chick color at day 11 that matters and at this age chicks are still very ornamented.

Assessing Whether Color Affects Chick Survival. Finally, we assessed whether chick color influenced chick survival during the parental provisioning period. Survival data were summarized into 5-d census period blocks and included survival data for up to 25 d after hatching completion, as in ref. 35. We used a mixed-effects Cox model with brood as the random effect and hatching order and chick color (PC1) as fixed effects. We conducted this analysis for both unmanipulated broods and experimentally synchronized broods.

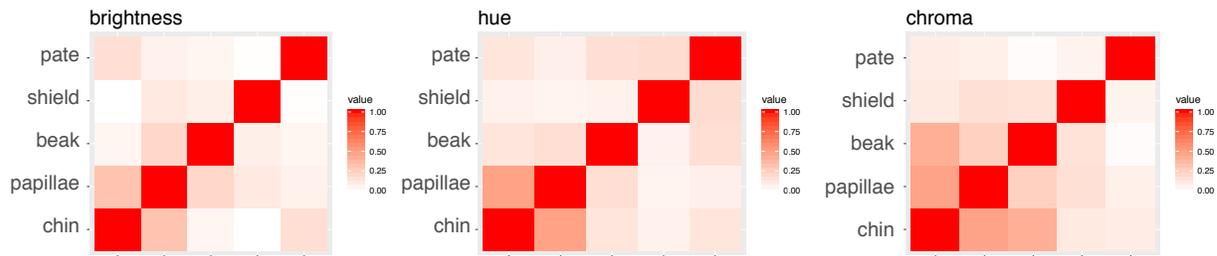
All data and analysis codes are archived at Dryad (61).

Ethics Statement. Field work was conducted under permits from the Canadian Wildlife Service and the University of California, Santa Cruz Institutional Animal Care and Use Committee.

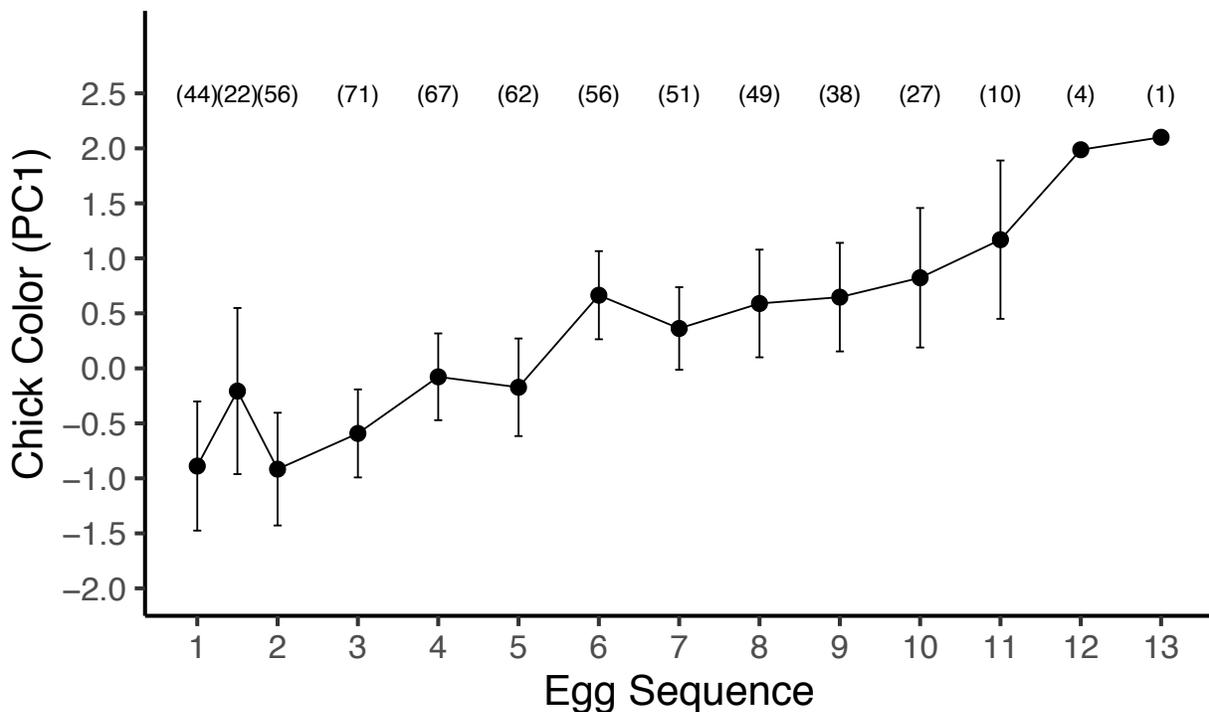
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Supplemental Figure 1: Correlations between color of different ornamental traits using three different metrics of color: (a) brightness, (b) hue, (c) red chroma.



Supplemental Figure 2: Relationship between egg laying sequence and chick color. Values in parentheses above indicate sample sizes. Egg sequence of 1.5 was assigned to the first two eggs in nests that were found with two eggs (thus we could not score laying sequence).

Supplemental Table 1: Principle component loadings (first three axes) with varimax rotation for color measures of static ornamental traits.

	PC1	PC2	PC3
Chin Chroma	0.441	-0.108	0.27
Chin Brightness	-0.192	-0.575	0.191
Chin Hue	0.408	0.118	0.204
Papillae Chroma	0.362	-0.026	0.303
Papillae Brightness	-0.337	-0.238	-0.075
Papillae Hue	0.393	0.067	0.083
Beak Chroma	0.317	-0.551	-0.254
Beak Brightness	-0.287	0.322	0.603
Beak Hue	0.142	0.418	-0.562