COMMENTARY

The mystery of ornate offspring

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Human curiosity, arguably our species' best feature, invites speculation about nature's myriad puzzles. Darwin's twin theories of selection (natural and sexual) provided a solid foundation for understanding how complex structures and behavior can evolve from simpler versions without divine assistance. We can posit plausible pathways by which traits that look engineered might have arisen on their own. But such conjecture, however creative, is only a "just-so story" until its components have been scrutinized and tested. In PNAS, Lyon and Shizuka (1) present a fascinating explanation for one such natural history gem, the startling bright colors of American coot (*Fulica americana*) chicks. Whereas most avian hatchlings have drab, camouflaged natal plumage, these marsh-dwelling youngsters look like floozies, with bright orange neck feathers and blue eyebrows against orange pate skin (Fig. 1). What possible ecological factors might have provided compensating benefits for genes directing such ornamentation? The authors' long-term study of coots in British Columbia tests predictions from theory and produces compelling evidence that the flamboyant traits probably evolved to serve the parents' interests within the context of resource competition within and, perhaps, between coot families.

The within-family pressure stems from general food uncertainty. Avian parents must commit to an integer number of eggs long before the family food budget can be assessed accurately, so the fit between supply and demand is often poor. In many species, they follow a general strategy known as brood reduction: The female lays more eggs than can typically be supported, relying on stepwise mortality to correct for the initial overproduction. The subsequent trimming of family size is facilitated by starting to incubate while the eggs are still being added (laying takes over a week for coots), a parental action that creates asynchronous hatching (because early-incubated eggs hatch days before their last-laid nestmates). The more senior coot chicks thus have a head start (size, coordination, etc.), enabling them to out-hustle the younger ones and survive the severe early cull (roughly half of hatchlings starve during the first week posthatching).

Fig. 1. Coot parents feed dependent young on aquatic insect prey via direct (bill-to-bill) transfers. Despite having potential control over which chick receives each item, parents mostly feed the closest individual for the first 7 to 10 d, during which half of the brood starves. That scramble competition phase ends abruptly when the two parents split the remaining brood, each adult skewing its food deliveries thereafter to favor the most ornamented chick in its subbrood. Image courtesy of Bruce Lyon (University of California, Santa Cruz, CA).

So far, this scenario sheds no obvious light on the fancy colors, because success, at this stage, hinges on speed, not beauty. Besides, many other birds practice brood reduction without chick ornaments. But coot brood reduction is exacerbated by an additional, external pressure, namely, the tendency for females to lay some eggs in the nests of coot neighbors. That is, many females outsource a few of their first-produced eggs before laying eggs in their own nests for which they provide all necessary service. The benefits for sneaking eggs into neighbors' nests are potentially great, because parental care is costly, and all those expenses are assumed by the hosts. Brood parasitism, famously practiced by Old World cuckoos on hosts of other species, is hard to detect, and thus less well understood with same-species victims. Might this odd habit account for the showy chick plumage?

One possibility is that such ornamentation might have arisen as part of the brood parasitism strategy, if

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it facilitates successful adoption by host parents. This scenario requires a preexisting parental preference for colorful nestlings that parasites exploit by giving them what they already like. The logic here is borrowed from mate choice models in the sexual selection literature, devised to account for exaggerated male traits (nightingale songs, peacock fans, etc.). Considerable research in recent years has uncovered various correlates of fancy male features, showing that the fanciest males provide valuable benefits to choosey females (better male parenting, genetically superior offspring, etc.) that help explain the female preferences in the first place. For the coot puzzle, the first step is to test whether it is the parasites that drive chick ornamentation, specifically whether the alien chicks tend to have brighter colors.

A subtler alternative is that the bright colors might be a host response to the threat of parasitism, part of an adaptive defense. If so, then an opposite pattern is predicted: Host chicks should be fancier than the aliens.

So, which is it (if either)?

To compare host vs. parasite chick coloration, the investigators (1) knew that the human eye can sort alien eggs from resident ones (a key detail confirmed by DNA identifications), so they simply nabbed pipping eggs (prehatching cracks appear 1 to 2 d ahead of emergence) and relocated them to a laboratory incubator to complete hatching. Each egg was enclosed in a light mesh bag that paired each new chick with its shell and status as host or parasite. Colorfulness was then quantified (spectrometric measures of key plumage and skin zones followed by principal component analysis to reduce covariation problems), revealing two key results. First, host chicks tend to be brighter than parasite chicks. Second, chicks from eggs at the beginning of a female's laying sequence tend to be duller than those produced later. The fanciest chicks are also the youngest runts.

This combination of color/rank patterns dovetails neatly with subsequent behavioral changes by the host parents. As noted above, the clutch hatches asynchronously (spanning almost a week), and the brood swims about with the two parents, which find and then pass aquatic food items over to the nearest chick. Such scramble competition confers a major advantage to slightly older and more agile youngsters, because they can maintain closer proximity. And most of these senior brood members are resident (host) chicks, simply because parasitic laying must lag behind that of hosts (the interloping female must first ascertain whether the host has begun producing eggs before she can sneak hers into the pile). Earlier work by these same authors (2) showed that host parents use this detail to imprint on their own chicks' signature traits (appearance and/or vocalizations) to gain a bit of discriminatory power. During that early phase, food allocations are unequal (albeit, not by any detectable parental bias), generally to the detriment of parasite brood members taking the brunt of the acute food shortage. As parasites starve, the hosts' burden is lightened.

After a week to 10 d, the host parents dramatically overhaul their own feeding rules with two behavioral shifts that further handicap parasites and boost the prospects of their own junior chicks. The surviving conglomerate brood is split in two, with one traveling henceforth with mom, the other with dad. Simultaneously, color-based parental favoritism activates, and each parent begins overtly promoting the most ornamented member of its subbrood (delivering 80% of its food morsels to that individual). By now, the early-fed senior chicks can mostly feed themselves, but juniors that were underfed during the scramble competition still need help. The bright colors work against the remaining brood parasites: Because they emerged from their mother's first-laid eggs, they tend to be dull-looking. In the end, both the early-fed seniors and the fanciest juniors are likely to be host offspring.

This system is particularly interesting for the way in which parents reverse their priorities midway through the rearing process. At first, they act in a way that facilitates chick mortality, with both parasite and host chicks dying. Then they become highly solicitous of one underfed survivor per parent, the opposite of the previous laissez-faire parenting. If there are other examples of parents switching feeding behavior like this, I am unaware of them.

The combined features of this complex system address a more general problem, namely, which generation controls parental investment. Offspring traits (both morphological features like plumage and behavioral ones like begging signals) that influence parental food allocations have been somewhat controversial in this respect. The classical view of parental care depicted the adults as benevolent despots that worked as hard as possible to ensure that all offspring would survive and thrive. In the 1940s, Lack (3) laid out the argument for brood reduction (the overproducing of eggs in tandem with engineering asynchronous hatching) as a remedy for food unpredictability. Later, it was pointed out (4) that parents can sometimes benefit from withholding effort from the current brood if doing so extends the parents' reproductive lives. Still, nobody was seriously questioning that the parental generation exercises hegemonic power over their young, but, in the 1970s, Trivers introduced parent–offspring conflict theory, proposing that offspring may have considerably more leverage than previously imagined (5). Without specifying just how feeble offspring can manipulate parents to do their bidding beyond what the parents would have done anyway (Trivers offered "psychological weaponry," such as tantrums), the scientific community's response to that argument was more enthusiastic than rigorous (6). In that context, it is interesting that all of the components of the Lyon and Shizuka (1) argument for coot coloration derive from adult traits. A given chick has no say about how many eggs are laid (and by whom), its rank in the laying order, the nutritional and hormonal contents of its yolk, when incubation begins, or whether parents will play favorites after everyone hatches: That entire suite of traits belongs to the parental generation (mostly the mother). Coot chicks seem to be pawns in this chess game, at least so far as we know to date.

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