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Communal Breeding: Clever Defense Against Cheats

High levels of conspecific brood parasitism are found in a communally breeding bird, with implications for the evolutionary links between brood parasitism and communal breeding. It also uncovers a novel egg recognition mechanism hosts use to foil brood parasites.

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Avian breeding systems often reflect a mix of cooperation and conflict over allocation of the costs and benefits of parental care [1–4]. This interesting juxtaposition of cooperation and conflict is particularly evident in the communally breeding birds, where two or more females lay eggs in the same nest and typically cooperate to raise the offspring. Beneath the veneer of group cooperation often lurks severe competition among females within the breeding group to maximize their share of reproduction [5,6]. The resolution to these conflicts results in communal breeding systems that range from nearly egalitarian — in terms of shared costs and benefits — to those that border on parasitism [5,6]. Conflicts over the costs and benefits of parental care are taken to the extreme in another breeding system in which one female lays eggs in another female's nest but fails to provide any subsequent parental investment — brood parasitism. Both of these strategies — communal breeding and brood parasitism — are widespread in birds, although usually they do not co-occur in the same species. Common threads between these two breeding systems include multiple females laying eggs in a single nest and the egg tossing behavior used to control whose eggs then remain in the nest [6,7]. The difference has to do with who pays for the subsequent cost of parental investment: do all females share the cost, or do some cheat on investment? While theory suggests potential evolutionary links between brood parasitism and some forms of communal breeding [1,8,9], these ideas have been difficult to test empirically. A recent study in Current Biology by Christina Riehl [10] adds a new beam to the proposed bridge between parasitism and communal breeding. Riehl demonstrates for the first time high levels of conspecific brood parasitism in an obligate communal breeder and also reveals a novel mechanism that birds use to foil many instances of brood parasitism.

A brief description of the strange reproductive antics of anis and their relatives is necessary to put the new discoveries into context. The Old World cuckoos are famous for their brood parasitic habits but the four species of non-parasitic New World cuckoo in the subfamily Crotophaginae — three species of ani (Crotophaga spp.) and the guira cuckoo (Guira guira; Figure 1) — have become textbook examples for their communal breeding habits. The four species vary in subtle ways, but Riehl's observations of greater anis (Crotophaga major) capture the essential details of communal breeding in this group [11]. Breeding groups typically comprise two or more pairs of birds that join together to cooperatively rear offspring in the same nest. An intriguing aspect of communal breeding — both in the Crotophagine cuckoos and in some of the other communal breeders as well [6] — is that nesting females remove eggs of other group members to increase their share of the group's reproductive output. Females simply eject eggs from the nest until they themselves have started to lay eggs. This egg removal synchronizes laying among females and, although the egg-tossing females often end up with a few more eggs in the clutch, reproductive skew tends to be fairly low [5].

Riehl [10] has now shown that the females outside of the group also try to get in on the game through conspecific brood parasitism — they lay eggs in nests without contributing to later parental care. To document the occurrence of brood parasitism, Riehl obtained maternal DNA by swabbing the surface of freshly laid eggs [12]. A maternal genetic signature (as opposed to genotyping the parasitic offspring themselves) makes

Figure 1. Cuddly but competitive.
The four members of the subfamily Crotophaginae, including the guira cuckoo (*Guira guira*) shown here, are all communal breeders where several females lay eggs in the same nest and then cooperate to raise the offspring. However, competition is also rife and females toss each other's eggs to control the skew in maternity. (Photo: Bruce Lyon.)

identification of brood parasites straightforward — any egg whose maternal genotype differs from those of all breeding females in the social group is from a brood parasite. An analysis based on 12 polymorphic microsatellite DNA markers revealed high levels of conspecific brood parasitism — 40% of nests were parasitized and 7% of eggs in the population were laid parasitically. These are on the high end of the range of frequencies reported for other birds [13], which suggests that parasitism is an important component of reproduction. Further studies are now needed to determine the identity of the brood parasites, and to investigate how exactly they benefit from parasitism. In theory, a variety of benefits are possible [7] and it will be interesting to see whether female anis gain benefits that are uniquely connected to aspects of their communal breeding habits.

In many species, the costs of brood parasitism have led to the evolution of host defenses such as egg rejection [14,15], and greater anis are no exception. Host anis removed many

of the parasitic eggs added to their nests. In terms of cognition, rejection of parasitic eggs seems paradoxical because anis appear to be unable to distinguish their own eggs from those of other group members. For example, when females toss eggs before they themselves lay, as is the case for within-group egg tossing, no egg recognition is required. How then can anis recognize and reject parasitic eggs added to their nest well after laying has begun? Riehl [10] proposed and tested a fascinating mechanism — temporal change in egg appearance. Freshly laid ani eggs are whitish, due to a covering of the chalky calcium carbonate polymorph vaterite [16], but over time change to a bluish color as the covering wears off — a built-in freshness indicator. Consequently, once incubation has begun and the hosts' eggs have changed from white to blue, any fresh white eggs added to the clutch by a brood parasite would stand out, and this could help anis discriminate parasitic eggs.

Riehl [10] conducted an experiment to test this idea, but the temporal

change in egg color added an interesting twist to the standard egg addition experiment used to test for recognition. In an elegant two-factor design, Riehl added either fresh (white) or incubated (blue) foreign eggs into fresh white clutches of eggs or blue clutches at later stages of incubation (Figure 2). In the two treatments where the parasitic eggs were synchronous with the host, and therefore similar in appearance (Figure 2), the hosts accepted the experimental parasitic eggs. However, in the two treatments where host and parasite eggs differed in appearance because of synchrony differences (Figure 2), many parasitic eggs were rejected.

A second clever experiment confirmed that anis do not recognize their own eggs *per se*. A single fresh host egg was removed from each of ten nests, kept in isolation for a week so that its color did not change, and then returned back to its home nest, at which point the host eggs left in the nest had changed color. Many of the hosts rejected their own egg that now differed in appearance from the rest of their clutch — confirmation that anis do not recognize their own eggs but simply reject eggs that differ in appearance. The changing color of eggs allows the communally breeding anis to bypass constraints on recognizing the eggs of individual females and instead use a simple color cue to discriminate foreign eggs. Earlier speculation on the unusual chalky vaterite covering of Crotophagine eggs suggested that it might enhance eggshell strength [16] but Riehl's [10] findings now suggest a possible signaling function. Intriguingly, the one other example of temporal color change in eggs that we are aware of also occurs in a communal breeder, the greater rhea (*Rhea americana)* [17], but whether this color change serves a signaling function is currently unknown.

Riehl [10] concludes from her experiments that anis do not know their own eggs but instead egg discrimination is based on rejection of the minority type that differs from the rest of the clutch, or 'recognition by discordancy' [18]. However, the color change aspect may complicate this interpretation because a third recognition mechanism is possible — anis may be able to keep track of approximately what color eggs should be at different stages
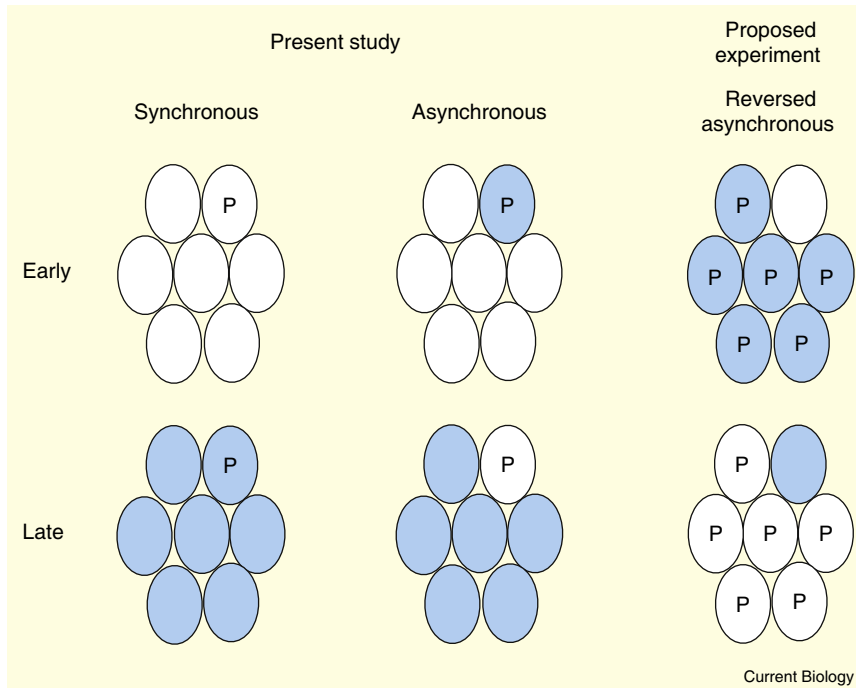
Figure 2. Experimental test for mechanisms of egg recognition in a species with eggs that change color over time.

The four treatments on the left and center were done in the study by Riehl [10]; the two treatments on the right are proposed experiments. Parasitic eggs, indicated by a 'P', were only rejected in the two treatments where the parasitic eggs differed in appearance from the host eggs, confirming that hosts use differences in appearance to recognize eggs. An issue that remains to be tested is whether hosts simply reject the rare type that differs or whether they know that eggs should change from white to blue over time and target eggs that differ from expectation, regardless of their frequency. The two experiments to the right permit a test of the latter hypothesis.

of incubation (i.e., white early on and blue later) and reject those that are not the right color, irrespective of their frequency in the clutch. This mechanism could be distinguished from discordancy by a simple experiment: repeat Riehl's asynchrony experiment but also alter frequencies so that host eggs become the minority type (Figure 2). If hosts reject the minority type, discordancy would be supported, but if they still reject the foreign eggs, the third hypothesis we propose would then have to be considered and tested. Because discordancy has never previously been found in birds, despite numerous tests [19], experimentally manipulating host and parasite frequencies would be well worth the effort.

Riehl's study [10] shows that greater anis must resolve the reproductive conflicts that arise within communally breeding groups while at the same time defending against cheaters from outside the group. Evolutionary connections between brood parasitism and communal breeding that have long been suspected but remain poorly understood. Seventy years ago Davis [8] focused a lengthy review entirely on the evolution of communal breeding in the Crotophagine in the context of brood parasitism. Because the group is embedded in a group of parasitic birds, the cuckoos, Davis asked whether communal breeding might be a stage in evolution of brood parasitism but concluded it was not — it is its own stable offshoot [8]. Nonetheless, the new evidence of the coexistence of parasitism and communal breeding within the same species [10] suggests a more immediate connection between these two breeding strategies. The Crotophagine birds thus offer a rich system for testing recent theory on how parasitism and communal breeding could turn out to be subtle variations on the same reproductive theme [9,20].

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