When cooperators cheat

A study of a cuckoo species that usually shows cooperative nesting behaviour, but sometimes cheats at parenthood by laying eggs in others’ nests, reveals the benefits that have shaped the evolution of this parasitic tactic. See Letter p. 96

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The evolutionary conditions that drive cheating versus cooperative nesting tactics in birds are a major focus of interest in animal-behaviour research. On page 96, Riehl and Strong report a study of a cuckoo species called the greater ani (Crotophaga major), which sometimes displays a cheating behaviour when nesting called conspecific brood parasitism, in addition to cooperative nesting behaviour. The authors tracked the identity of females and the eggs in their nests to assess the costs and benefits of this alternative parasitic tactic.

Conspecific brood parasitism occurs when a female lays her eggs in a nest belonging to another member of the same species, but does not provide any offspring care. By contrast, in one specific form of cooperative breeding, the care and defence of the offspring in a nest are shared between two or more females (and, in some species, their mates). Crotophaga major is a rare example of a species that exhibits both types of behaviour in the same population, providing an opportunity to examine the evolutionary relationships between these two tactics.

The authors tracked nests in the wild over 11 breeding seasons, and used DNA analysis to identify the birds in each nest and determine the mother of each egg, using techniques that included non-destructive extraction of DNA from eggshell surfaces. Riehl and Strong observed that females almost always show cooperative breeding behaviour at the start of the breeding season. If predators destroyed a nest, the authors found that some affected females pursued a parasitic strategy in the same breeding season, whereas others waited until the next year’s breeding season to lay more eggs and nest cooperatively (Fig. 1). The authors report that either cooperative breeding combined with parasitism after nest failure or solely cooperative breeding provided similar numbers of surviving offspring. The parasitic females laid more eggs than the solely cooperative females, but the death rate of parasitic eggs was higher than that of non-parasitic eggs, owing to host rejection.

The authors found that any given individual used just one of these two alternative breeding tactics repeatedly over many cases of nest loss. Three explanations are usually given for why conspecific brood parasitism occurs. One possibility is the ‘super mother’ scenario in which females develop eggs in excess of the optimal number for their own nest, and lay the extra eggs in other nests. This is a successful strategy in some birds and insects. Another explanation, which has had little support, is that the females are specialized parasites that never construct their own nest. The third is that females are making the best of a bad situation in which parasitism is a last resort taken by a female that would otherwise have nested in the usual way. Riehl and Strong provide support for this hypothesis.

Why Crotophaga major individuals are not normal parasitic breeders except as a response to nest predation, or why they do not pursue both parasitism and cooperative nesting in the absence of nest predation, is a mystery. Perhaps the benefits of cooperative breeding for egg survival are so great (relative to the lower survival of parasitic eggs associated with host rejection) that it has evolved to be the default option; this would explain why parasitism is pursued only after nest failure, rather than as the sole option of choice or pursued concurrently with cooperative nesting.

More than 300 bird species cooperatively breed, and 200 show conspecific brood parasitism, but few species are found to exhibit both. It has been proposed that cooperative breeding and parasitism might represent extremes of offspring care by a female that contributes eggs to a nest already occupied by another female. Cooperative breeding might have evolved directly from parasitism if a host provides incentives to entice a female parasite to remain at the nest and cooperate. However, Riehl and Strong show that the relationship between cooperative breeding and parasitism is
more complicated than was previously thought, because parasitism seems to have evolved as part of an existing system of cooperative breeding, rather than the other way around. Intriguingly, the same single factor of high levels of nest predation drives both behaviours. Cooperative breeding is favoured over solitary nesting (in which a single female and her mate care for the nest) because of predator pressure.

The idea that genetic relatedness between individuals can affect the evolution of social interactions has had a central role in our understanding of cooperative breeding in many species, and some models suggest that kinship might also have a role in the evolution of brood parasitism. A brood parasite might actively target kin to increase the survival of host eggs by buffering their predation risk as a result of adding parasite eggs, or hosts might accept eggs of non-nesting kin because that is the parasite’s only opportunity to reproduce. Parasitism might, therefore, sometimes have a cooperative aspect, blurring the distinction between cooperative breeding and parasitism when kin are involved. However, Riehl and Strong show that kinship does not play a part in the parasitism of C. major, because the relatedness of the hosts and parasites was not greater than that in the general population. This meant that the authors could focus on the evolution of nesting tactics without having to consider the influence of kinship.

Why specific C. major females pursue parasitism is unknown. The observation that individual females consistently used this tactic each time their nest failed, whereas others did not, suggests that there might be a heritable basis. Alternatively, parasitism might be shaped by other factors, such as development, learning or physiology. Perhaps certain females consistently provide less parental care than others in cooperatively breeding nests, and therefore have more resources in reserve for parasitic egg laying if their nest is destroyed. Another possibility is that some females avoid parasitism and reserve resources to meet the higher demand for parental care in their own future nests. Quantifying the costs of parental care and the energetic demands of egg laying would help to shed light on this. Following these behaviours across the entire lifetimes of C. major could determine whether the benefits of parasitism across breeding seasons found in this study scale up to benefits in lifetime reproductive success in this fascinating species.

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This article was published online on 27 February 2019.