Ontario Gray Jays Help on the World Stage: Part 2

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In Part 1 of this article (*Ontario Birds* 20: 130–138), I stated that a common Ontario bird, the Gray Jay (*Perisoreus canadensis*), provides what may be a useful insight into the worldwide phenomena of communal breeding and allofeeding in birds.* I pointed out that in Algonquin Park about 20 percent of Gray Jay pairs have a single nonbreeder associating with them at the beginning of the breeding season in late February. This is the basic recipe for communal breeding to occur (nonbreeders still at home with Mom and Dad) but nevertheless, in Gray Jays, the nonbreeders do not feed nestlings. This is puzzling because many helpful advantages have been proposed for communal breeding and Gray Jays seemingly could benefit much more than most birds. After all, they nest in hostile, late-winter conditions with no obviously reliable food in the forest. Why wouldn't a nesting pair of Gray Jays benefit from an extra forager? Why wouldn't the nonbreeder benefit as well, either by gaining valuable experience, or by improving the production of younger siblings, each carrying half its genes (the same fraction that its own young would have if the nonbreeder could breed itself). Even more surprising, the breeding pair actively *harasses* any nonbreeder that may be present, even when the nonbreeder is one of its own offspring from the year before. I ended Part 1 by inviting readers to formulate their own hypotheses to answer these questions before I summarized, in this issue, the explanation proposed by me and my Gray Jay partner, Tom Waite, of Ohio State University (Strickland and Waite 2001).

Let me take up the story again from Part 1 by repeating that, for years, I was completely at a loss to understand the absence of allofeeding in the Gray Jay nestling period. In 1994, however, Tom Waite made the amazing discovery that non-

* Found in over 200 species around the world (Brown 1987), mostly in tropical areas and especially in Australia, communal breeding is characterized by three or more adults participating in at least some parental activities, including courtship feeding, nest building, attacking nest predators, and feeding young. Allofeeding is a feature of communal breeding and refers to the feeding of young birds by adults other than their parents. Communal breeding and allofeeding are both commonly and misleadingly called "helping" on the (often unsubstantiated) presumption that they are beneficial to the individuals receiving or exhibiting such parent-like attention.

breeding Gray Jays sometimes feed young in the fledgling period (Waite and Strickland 1997). This was a thunderbolt! After all, why would nonbreeding Gray Jays refrain, or be prevented, from helping in the wintry nestling period and yet be allowed to help in the fledgling period? Why would "helping" be permitted to begin precisely when new food is starting to become available and extra help from a nonbreeder would seem to be less important?

After Tom's initial discovery, we observed four more cases of nonbreeders (at least one of them completely unrelated to the family involved) starting to feed young in the fledgling period. We have also observed at least one case where a nonbreeder refused to feed his younger siblings, even though he was not prevented from doing so by the adults and in spite of the fact that the fledglings often begged at him. The fact, then, that nonbreeding Gray Jays may or may not feed young in the fledgling period but apparently never do so in the nestling period (when the need is apparently so much greater) forced us to conclude that such feeding cannot be particularly important for successful reproduction in this species. It finally dawned on me that the so-called "help" that nonbreeders can give is probably not helpful at all—at least not in Gray Jays. I had been fooled all those years by the use of the word "helping" and its unquestioned—at least by me—implication that feeding another bird's young necessarily had to be beneficial. Still, facing up to my error did nothing to explain why adult Gray Jays seemed actively to prevent "helping" in the nestling period and only relax their opposition in the fledgling period. After all, it's one thing to have little or no need for the allofeeding services of a nonbreeder; it's quite another to go to all the trouble of actually shutting such behaviour down.

As we watched fledgling Gray Jays being fed by adults and nonbreeders in the late 1990s, we noticed something that suggested a possible answer to the mystery. I had spent many hours in the past watching Gray Jay nests and had always been struck by how infrequently the adults came to the nest and how, when they did come, that their expandable throats were always filled to overflowing. In marked contrast, feeding trips in the fledgling period seemed to be much more frequent and often seemed to involve very small amounts of food. The thought occurred to me that, in the nestling period, Gray Jay parents were doing their best to reduce trips to the nest to an absolute minimum. They were doing this by preventing any nonbreeder from going to the nest and, on their own visits, by bringing the biggest loads possible, thereby minimizing the number of trips they needed to make to the nest. In the fledgling period, on the other hand, it seemed that Gray Jays were not motivated to minimize the number

of feeding trips. The adults did not stand in the way of any nonbreeders who wanted to feed or otherwise visit the fledglings and they themselves often brought small amounts of food in a consequently large number of individual feeding trips.

But what could account for such a dramatic switch from minimizing visits to nestlings to suddenly relaxing this constraint in the fledgling period? The answer, we suggest, is that there is a predator (or predators) that finds nests by observing flights to the nest and/or hearing the sounds of nestlings begging and being fed. The predators, furthermore, are probably flightless or otherwise much less of a threat to fledglings than to nestlings. That would explain why Gray Jay parents work so hard to minimize visitation to nestlings but then abandon this vigilance as soon as the young birds leave the nest. Everything seemed to fit. We even had a likely predator in the Red Squirrel (*Tamiasciurus hudsonicus*). Although squirrels are not popularly thought of as meat-eaters, more and more studies have been showing that the Red Squirrel, in particular, is a devastating predator on eggs and nestlings, and even on young mammals. Even worse, Red Squirrels are so common in the coniferous forest habitats of the Gray Jay (sometimes at more than one per hectare) that it is difficult to imagine how a jay nest can escape detection by the local squirrels in the 20 days from first egg to hatching and then the 23 day nestling period.

Coming up with a plausible hypothesis, however, is not the same thing as actually testing it. Fortunately, we were able to evaluate our idea by comparing Gray Jays with the many other corvid species that have been studied in detail, including a few with behaviour similar to that of the Gray Jay. This, then, was the basis of the paper Tom and I published in the *Canadian Journal of Zoology*. We proceeded in six steps, as follows:

Step 1. The fundamental premise of our predator avoidance hypothesis was that adult Gray Jays would succeed in reducing the number of visits to the nest if they prevented nonbreeders from going there. For all we really knew, however, it might not make any difference. If adults needed to feed the young less often, for example, because the nonbreeders were doing some of the work for them, the total number of visits to the nest might well be the same, whether or not the nonbreeders were permitted to participate. Ideally, the way to settle this question would be to compare the feeding visitation rates of Gray Jays assisted by nonbreeders with pairs that were unassisted. Unfortunately, we couldn't do such a comparison because Gray Jay pairs are never assisted by nonbreeders in the nestling period. Settling for second best, we compared the visitation rates of assisted versus unassisted pairs in other corvids where both situations really do occur. We found relevant data for six species and, with-

out exception, the visitation rates were lower at unassisted nests than at assisted nests. Therefore, it seems highly likely that the same would be true in the Gray Jay, and that Gray Jay parents really do lower the visitation rates to their nests by preventing nonbreeders from going there. The fundamental premise of our predation avoidance hypothesis is, therefore, likely to be correct.

Step 2. Our second step was to take a close look at the hostility Gray Jay parents show to their associated nonbreeders in the nesting season to see if it is consistent with our hypothesis. We found, for example, that in the breeding season, Gray Jay nonbreeders were much more likely than before the breeding season to be off by themselves. And, when they actually were with the adults, the nonbreeders were chased much more during the nesting season than beforehand. In addition, such chasing was much more frequent when the nonbreeders were close to the nest than when far away. Interestingly, it made little difference whether the nonbreeders were the young of the adults from the previous year or unrelated strangers. Both nonbreeder classes were treated in a hostile manner in the nesting season and both were effectively excluded from the nest area. All of these findings were more consistent with our predation avoidance hypothesis than with other possible ideas to explain the nesting season hostility of breeders towards nonbreeders, including their own young.

Step 3. In the remaining steps of our evaluation, we examined four predictions stemming from our predation avoidance hypothesis. In general, we reasoned that if the suppression of allofeeding in the nestling period of the Gray Jay is driven by the advantage of lowering the number of predator-attracting visits to the nest, then the Gray Jay and other jay species with similar behaviour should do other things as well to lower nest visitation. For example, these jays might be expected to have smaller clutches than jays that do not suppress allofeeding. All things being equal, fewer mouths to feed should mean fewer visits to the nest and this would make another contribution to hiding the nest from predators. This idea originally was suggested by Skutch (1949) as an explanation for the very small clutches (often only two eggs) of birds living in neotropical forests, a habitat well known for its extremely high nest predation rates. It turns out that the Gray Jay and similar species that suppress allofeeding in the nestling period do indeed have significantly smaller clutches than jays that permit allofeeding.**

Step 4. Skutch (1949) also described how some tropical bird parents, such as antbirds (Formicariidae), seemed to bring the largest food

** This is a bit of an oversimplification. For a more complete discussion of the significance of clutch size in jays, see Strickland and Waite (2001).

items that their nestlings could possibly swallow. He specifically suggested that the adults were maximizing their food load sizes so as to minimize the frequency of their predator-attracting nest visits. Similarly, we predicted that Gray Jays and other corvids that suppress allofeeding should—if predator avoidance is the critical factor—also maximize their food load sizes. Sure enough, this appears to be the case. The adults of jays that suppress allofeeding apparently load up as much as possible when they are feeding young and consequently visit them much less frequently.

Step 5. We proposed that Gray Jays suppress allofeeding in the nestling period because of the need to minimize predator-attracting visits to the nest. This suppression is relaxed after the young fledge, presumably because the predator(s) no longer poses a threat to the young when they can fly. If it is also true that adult Gray Jays suppress their own feeding visitation rates in the nestling period because of the same need to avoid attracting predators, then we might expect this feeding rate suppression to be relaxed after the young fledge—just as the suppression of allofeeding by nonbreeders is relaxed at the same time. Not many bird species have had their fledgling feeding rates measured (we found 14), but in almost all of them, adults feed fledglings at a faster rate than nestlings. The feeding rate increase from the nestling period to the fledgling period was much greater for the Gray Jay than for the other species, however. We also were able to show that the big increase was due, not to an exceptionally high feeding rate in the *fledgling* period but, rather, to an exceptionally low feeding rate in the *nestling* period. Once again, our comparisons with other species supported the idea that Gray Jays do whatever they can to minimize feeding visits to their nests.

Step 6. The final prediction stemming from our predation avoidance hypothesis was that the Gray Jay and other corvids that prevent allofeeding would have less ability to confront nest predators than jays that allowed allofeeding. Our reasoning was that if Gray Jays and similar species could not successfully drive predators away, then they should do everything possible to avoid the predators detecting their nests in the first place. To assess defensive abilities of different corvids, we compared their body weights and group sizes. Sure enough, the Gray Jay and other species that suppress allofeeding are significantly smaller and live in smaller groups than species that allow allofeeding. The Gray Jay, in fact, is the smallest jay that regularly has nonbreeders associating with breeding pairs and rarely does it have more than one nonbreeder per pair, for a typical group size of three (Strickland 1991). If you were a nest predator, you might not be deterred

Figure 1: Nonbreeding Gray Jays are excluded from the nest area by the breeding pair. Such behaviour probably helps to minimize the number of predator-attracting trips to the nest. Photo by *Dan Strickland.*

by three wimpy little Gray Jays, each weighing 75 grams or so, but you might very well be intimidated if you were trying to get to a nest defended by 10 or 11 Brown Jays (*Cyanocorax morio*), each weighing 210 grams.

Overall then, we found strong inferential support for the idea that Gray Jays and other species that suppress allofeeding in the early parts of their nesting cycle do so to reduce the risk of predators finding their nests. Indeed, we see the suppression of allofeeding and allowing it to occur as alternate anti-predator strategies. For species like the Gray Jay that are small and live in small groups, the best strategy is to do everything possible to conceal the nest. This means building it to be as inconspicuous as possible, of course, but it also means reducing trips to the nest that could tip off the location of the nest to predators. Feasible measures include any or all three of: (i) having a small clutch size (to lower the number of mouths to be fed); (ii) maximizing food load size (to minimize visitation frequency); and (iii) preventing nonbreeders from feeding nestlings or otherwise visiting the nest.

For large species that occur in large groups, however, the best strategy may be just the opposite—actually to enhance allofeeding. The food brought by the nonbreeders

may not be very important but, merely by bringing it, especially in small quantities in numerous trips, the nonbreeders are that much more likely to be near the nest and therefore to detect and confront any approaching nest predators.

Tom and I believe that the predator avoidance hypothesis provides a reasonable and well-supported explanation of why Gray Jay parents actually spurn the "help" that nonbreeders could bring to the task of feeding nestlings under difficult, late-winter conditions. And with it, we think we have solved this perplexing aspect of Gray Jay behaviour that had stymied me for many years. The real significance of the predation avoidance hypothesis, however, may lie in its ability to help understand much more than Gray Jay behaviour. In 1961, A.F. Skutch (who else!) sought to explain the rarity of communal breeding in birds by suggesting that the increase in nest traffic caused by allofeeders would be dangerously attractive to predators (Skutch 1961). Skutch believed that communal breeding therefore tended to be confined to birds with inaccessible nests or which were large enough (like corvids) to dissuade most nest predators. Skutch accordingly came up with the predator avoidance hypothesis long before we hit upon the idea in a slightly different context to explain Gray Jay behaviour. Almost no one picked up on Skutch's idea, however, and even Skutch himself apparently failed to realize the full potential of his idea to explain the presence and absence of communal breeding around the world.

Recall from Part 1, for example, that the Green Jays (*Cyanocorax yncas*) of Texas are not communal breeders but those in Colombia are. Might this difference be explained by different suites of predators in the two locations? Alternatively, or as additional contributing factors, the smaller size of the disjunct Central American races, including the Texas race (Gayou 1986, Madge and Burn 1994), and their smaller group sizes, may make the northern birds less able to deter nest predators and less likely to allow allofeeding than South American forms that are larger and occur in large groups.

Similarly, allofeeding in the nestling period of the Florida Scrub-Jay (*Aphelocoma coerulescens*) may be permitted by the scarcity of squirrels in that species' oak scrub habitat (G. E. Woolfenden, pers. comm.), and the prevention of allofeeding in the nestling period of the Western Scrub-Jays (*A. californica*) of Oaxaca may be related to the probable presence of squirrels in the pine-oak forests used by that population (Hall and Kelson 1959, Burt and Peterson 1993). On a broader scale, the absence of allofeeding in all mainland forms of the highly social white-eyes (Zosteropidae) and its occurrence in only a few island species (Skutch 1999) may correspond to mainland-island differences in exposure to predators. Similarly, the abundance

of allofeeding species in Australia, including very small ones (Dow 1980, Brown 1987), and the very high nest-visitation rates that have been reported in some of them (Dow 1978, 1980) may be related to that continent's lack of squirrels and possibly other diurnal nest predators that hunt in a similar manner.

We don't know if the predation avoidance perspective will be the key to understanding why allofeeding is distributed around the world the way it is. Nor do we know if it will explain why the behaviour is so common in Australia. But clearly, four decades after Skutch first underlined its importance, it is not too soon to ask if predation or its absence may be a possible explanation for the existence of so many allofeeding species down under. And if, as we suspect, it turns out that the absence of diurnal, squirrel-like predators in the island continent goes a long way towards clearing up the big Australian question, we will be well pleased. A little bird on the other side of the world, in far-off Ontario, will have provided a useful insight. Or to put it another way, Gray Jays may not allofeed very much but, when it comes to understanding why some birds do and some birds don't, maybe they can help a lot.

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