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Natural selection: Fair weather cooperators

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<https://doi.org/10.1016/j.cub.2022.09.050>

An impressive long-term study of Greater Ani birds reveals fluctuating selection for group size. In wet years, with abundant food, larger groups enjoy greater protection from predators. In dry years, however, larger groups suffer greater nestling mortality relative to smaller groups.

Understanding the maintenance of genetic and phenotypic variation within populations has long been a central goal of evolutionary biology¹. Of particular interest are cases where discrete alternative phenotypes or behavioral strategies are maintained in a population². Despite a common intuition that one strategy should be more successful and dominate over time, alternative tactics remain widespread in nature. Our best examples include alternative tactics of males and females during mating and offspring care^{2–4}. There is also increasing evidence for alternative life history tactics such as migratory behavior in birds^{5,6} as well as cannibalism and swarming behaviors in

insects^{7,8}. A study in a recent issue of *Current Biology* by Riehl and Smart⁹ provides an example of alternative tactics in a novel context, social group size. The 13-year study shows temporal variation in the optimal group size (of two versus three breeding pairs) for a bird, the Greater Ani (Figure 1). Importantly the authors measured the trade-offs that help explain the maintenance of these two discrete group sizes, discovering that El Niño and La Niña weather events impose group size-dependent risks of nest predation and nestling starvation.

Group size varies across social animals, in contexts ranging from large ant colonies and schools of fish, to smaller co-breeding groups found in mammals,

birds, and invertebrates¹⁰. There is a rich history of research on understanding the optimal group size in these contexts, as well as the resolution of conflicts within groups when resources are limited^{11–13}. ‘Optimal group size’ might seem to imply that there is a single optimum. However, the optimum may vary across habitats or time due to spatial or temporal variation in the costs and benefits of different group sizes¹⁰. In some cases, individuals may be making the best of a bad situation⁵ by adopting a group size that maximizes their fitness for the context in which they find themselves, even though this yields a lower fitness than if they had joined a group situated in better conditions. Alternatively, and more unusual, different



group sizes may yield equal fitness over the longer term when the trade-offs for different group sizes tend to balance out. The new research on anis provides rare evidence for this latter, balanced fitness scenario.

The Greater Ani is a joint-nesting species (multiple pairs cooperatively breed in the same nest) and is unusual in that reproduction and offspring are shared roughly equally among all group members¹⁴. As a result, any benefits and costs of group size are distributed equally across co-breeders¹⁵. Single breeding pairs are never successful (due to predation) and are rarely observed. Groups with four breeding pairs experience intense nestling competition leading to nest loss, so are also quite rare. This leaves groups of two or three breeding pairs as the only alternative tactics in the Greater Ani — Riehl and Smart⁹ show that a minority of nests fall into the latter category each year with 20% of nests (on average) containing three breeding pairs. In wet years, it pays to be in a group of three breeding pairs (more protection from predation), but in dry years these same groups have lower chick survival due to limited food resources. Because there is no nepotism or chick recognition, overproduction of chicks means that all individuals in groups of three breeding pairs suffer equally in harsher years. As a result, calculations of long-term fitness for individuals in each of these two group sizes reveal roughly equal fitness, and hence weak to little natural selection favoring either group size.

Previous work has shown that another alternative tactic (brood parasitism) may have a genetic basis in Greater Anis¹⁶, and it may be that choice of group size also has a genetic component. However, the authors suggest that there is also an environmental component to group size because individuals change groups across their lifetimes. This raises the question of whether there is sufficient behavioral plasticity for individuals to adjust their group size facultatively (and optimally) year-to-year based on environmental conditions. Groups of three breeding pairs remain in the minority, even in years for which they are the more successful — this raises the question of what constrains individuals in groups of two from abandoning their partners to form a larger group. Similarly, larger



Figure 1. Cooperative nest of Greater Anis.

A nesting group of Greater Anis at work, provisioning chicks. © Christina Riehl.

groups do not appear to eject a third breeding pair in drier years when they suffer reduced offspring provisioning; reducing group size would allow them to conform to the group size optimum for that season. Previous work has shown that these joint-nesting females are genetically unrelated¹⁴ so the inclusion of a sub-optimal third breeding pair cannot be explained as kin-directed altruism.

Why, then, would groups not dissolve and reform each year to optimize and conform to the more preferred group size? It is likely that the advantages of long-term affiliations are at play here because breeding groups stay together for four years on average, even up to a decade. There are cooperative benefits of these long-term affiliations — anis that have bred together previously show an increased reproductive synchrony and higher fledgling success¹⁷ plus a reduced probability that a female will completely skip breeding in a given year¹⁸. Ultimately, females could maximize their lifetime fitness by balancing the benefits of group fidelity with optimal group size choice when it comes time to occasionally switch groups. Just as individuals could (in theory) switch group sizes to optimize their personal fitness, breeding pairs could move within a heterogeneous

landscape to avoid risk or take advantage of resources. This study⁹ and previous work¹⁴ reveal much higher predation rates for nests on the shoreline compared with those in emergent vegetation surrounded by water. In fact, survival is so high at nests surrounded by water that the effect of group size on predation risk appears minimal compared with shoreline groups, where predation is intense and strongly associated with group size. Given that habitat type is a reliable cue for predicting the long-term risk of predation, and that birds stay put on a territory for several years, adaptive group size might be expected to vary across habitats. It would be interesting to calculate the expected lifetime fitness for birds that solely nest in emergent vegetation versus on the shoreline for each of the two breeding group sizes.

Helpers are also an interesting part of the story in Greater Anis, and have been a focus of alternative tactics in other species of birds^{19,20}. Helpers are non-reproducing adults that provision chicks and defend the nest from predators; some number of helpers (1–3) are present in ~20% of Greater Ani nests¹⁵. Riehl and Smart⁹ show a clear positive effect of helper number on group fitness, revealing that selection on group size is affected by

both breeding pair number and helper number. It would be interesting to know if fitness benefits of helpers are entirely independent of breeding pair number, or if helpers ameliorate the costs of a two breeding pair group in wet years or a three breeding pair group in dry years. While the overall group size (helpers plus breeders) did not vary across years in this study, the numbers of two versus three breeding pairs varied quite a bit; this raises the question of whether helpers 'fill in' vacancies to allow a group of two breeding pairs to take advantage of extra resources in a wet year. The behavioral flexibility of helpers means they could also move between groups to maximize direct fitness (e.g., future mates or breeding sites) and indirect fitness (e.g., helping raise siblings). Thus, helping behavior may be yet another intriguing alternative tactic for future study in the complicated social networks of Greater Anis.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Evolution: Divergent trajectories predate the origins of animals and fungi

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<https://doi.org/10.1016/j.cub.2022.09.047>

Animals, fungi, and their closest protist relatives comprise the clade Opisthokonta. Although they are comparatively closely related, animals and fungi have diverged greatly from one another. A new study demonstrates that the genomic features that are characteristic of animals and fungi arose even before the origin of these two kingdoms.

Animals and fungi are closely related. Well... not *that* closely related — they shared a common ancestor over 1 billion years ago^{1,2}. At first glance, humans and mushrooms do not share many characteristics, but when we dive a bit

deeper, there are notable similarities between animals and fungi. The clade that comprises animals, fungi, and their closest unicellular protist relatives is called Opisthokonta³, named after their shared characteristic of having a

flagellum at the rear of the cell (*opisthios* = rear, posterior; *kontos* = pole, i.e., flagellum). Although most fungal lineages have lost this appendage completely, when present the flagellum is at the back end of the cell and pushes the cell