Superb starlings swap helper and breeder roles with kin and non-kin

A 20-year field study of the African superb starling (*Lamprotornis superbus*) found striking evidence that birds often switch breeding roles from year to year by taking turns as 'breeders' or each other's 'helpers'. This reciprocal assistance was not explained by genetic relatedness (kinship) and required decades of observation to be detected.

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The problem

Cooperative breeding occurs when some individuals in a group forego reproduction and act as 'helpers' by feeding or guarding offspring of dominant 'breeders'. Globally, nearly 10% of the more than 10,000 species of birds breed cooperatively[1].

Helpers and breeders are often related, as expected from kin-selection theory, which highlights the effect of helping relatives on indirect fitness (the transmission of genes because of cooperation between family members). However, because almost half of cooperatively breeding bird species form groups with both kin and non-kin[2], helpers can also be unrelated to the offspring they feed. This suggests that helping has other benefits, including improving the helper's ability to survive by increasing group size.

It has long been contested whether reciprocity — the idea that helping promotes future reciprocal assistance — occurs in animals other than humans[3], and it is not generally considered an explanation for helping in cooperative breeders. Such helping is assumed to be unidirectional, with subordinates aiding dominant breeders and not vice versa.

The discovery

We sought to understand the benefits of helping in the superb starling (*Lamprotornis superbus*), a cooperatively breeding bird living in the harsh and unpredictable savannahs of East Africa. Between 2002 and 2021, we studied a population of starlings, cataloguing more than 12,000 helping events by 563 helpers at 410 nests, across 9 social groups over 40 breeding seasons. Because the starlings' social groups contain both relatives and non-relatives, we sought to identify the mechanisms that underlie cooperation in these 'mixed-kin societies'. We collected DNA from most, if not all, individuals in the population to examine genetic relationships, and gathered evidence for various proposed evolutionary benefits of helping. Did the birds preferentially help relatives? Did they help non-relatives even when relatives were available? Did they reciprocate help with specific individuals over the years?

Starling helpers preferentially aided related breeders (kin) but also frequently and consistently helped specific non-kin birds, even when related breeders were available. Surprisingly, kin and non-kin repeatedly formed reciprocal helping relationships by swapping breeder and helper roles during their lifetimes. This subtle but consequential pattern of reciprocity required decades of continuous observation to detect (Fig. 1).

Given the frequency of non-kin helping and the occurrence of reciprocal aid between kin and non-kin, helping seems to be stabilized mainly by benefits to direct fitness (an individual's lifetime reproduction). However, the sex and group membership of helpers also influenced the relative magnitude of direct and indirect fitness. For example, female starlings born in the group gained only indirect fitness because we never saw them become breeders, whereas reciprocal helping was more evident for immigrants of both sexes.

The implications

Future reciprocal aid has mostly been ignored as a possible benefit of helping among cooperative breeders. Although long-term reciprocal-helping relationships are more difficult to detect and measure than is kin-biased helping[4], experience-based helping decisions could have a key role in stabilizing cooperative societies. In humans, for example, extreme helping occurs in families, yet less costly reciprocal support through friendships remains essential to health and well-being. The cryptic reciprocity observed in starlings could have a crucial yet overlooked role in other cooperatively breeding societies, especially those with kin and non-kin collaborating in harsh and unpredictable environments.

Our study provides exciting future directions. Despite clear observational evidence of reciprocal helping, correlational data alone cannot directly demonstrate or measure causal mechanisms. For example, without experimental manipulation, it is impossible to know whether or how much starlings would alter their cooperative investment in birds that have stopped helping them.

Cooperative societies are networks of interacting individuals. To measure and model how social networks change over time, researchers must use automated high-resolution sampling of the interactions between all individuals. The resulting models could inform field experiments to manipulate and understand individual helping decisions.

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EXPERT OPINION

"The authors use a 20-year data set of behavioural observations combined with a deep pedigree to investigate helping decisions in the cooperative, plural-breeding superb starling. It is rare to find results supported by such a deep and detailed data set that are also statistically sound. The paper does an excellent job of exploring the different facets offered by the data and will be a valuable contribution to the field of cooperative breeding."

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FIGURE

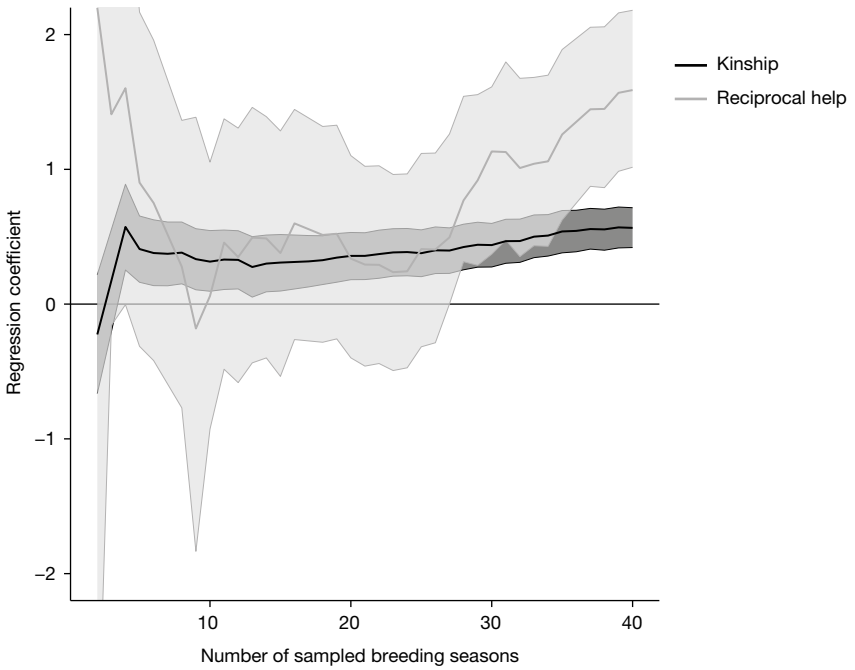

Figure 1 | Many more observations are needed to detect the effects of reciprocal help compared with those of kinship on helping rates in cooperative breeding. The superb starling (*Lamprotornis superbus*) shows cooperative breeding, whereby 'helpers' assist other 'breeders'. The discovery of reciprocity between helpers and breeders was made possible only by observations over many breeding seasons. Here, lines and shading show means and 95% Bayesian credible intervals for the estimated effects of kinship (dark grey) and reciprocal help (light grey) on helping rates. A kinship bias in helping is clear (the credible intervals are above zero) after only 3 seasons of observation, whereas 27 seasons were required to detect reciprocal helping. After 40 breeding seasons, reciprocal help is a better predictor of helping than is kinship.

BEHIND THE PAPER

I began this project on superb starlings at the start of my PhD more than 25 years ago. Wilson Watetu, my first field assistant, helped to collect much of the data over the next few decades. My PhD student Shailee Shah found that differences in group size are associated with differences in individual fitness and each group's long-term stability[5]. For most groups, reproduction was low, because the African savannah is harsh and unforgiving, with high rates of nest predation and nestling starvation. We realized that resident starlings could increase group size only by admitting unrelated immigrants that were allowed to breed almost immediately. These non-kin birds stabilized and shaped the structure of these mixed-kin societies. But why would individuals help these new unrelated group members? Undergraduate student Arden Berlinger began to explore this important question. The answer finally emerged from a series of analyses done by my PhD student Alexis Earl and collaborator G.G.C.

D.R.R.

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FROM THE EDITOR

In many birds, helpers delay their own reproduction to raise the young of others. Because the breeders are typically related to them, theory suggests that helping results from kin selection. But other theories hold that helping could be driven by reciprocal altruism. Both mechanisms are true, as shown by a study of superb starlings in Kenya, illustrating the importance of long-term field studies, and the difficulties of fitting theory to the real world.

Henry Gee, Senior Editor, *Nature*