Cooperative breeding and the evolutionary coexistence of helper and nonhelper strategies

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In some species individuals altruistically delay their chance of reproducing to help others raise their young. This is commonly referred to as cooperative breeding and is widespread across the animal kingdom, occurring in insects, crustaceans, fish, birds, and mammals, including humans (1, 2). This behavior has puzzled biologists for decades because, why should one individual help another at an expense to itself (3–5)? Surely natural selection should favor individuals that maximize their own reproductive success, and not that of others (3, 4). In PNAS, Wang and Lu (6) address how altruistic and selfish strategies can stably coexist within populations, an issue that remains poorly understood in cooperative breeding animals.

In the mid 1960s, the problem of how altruism can evolve was largely resolved by W. D. Hamilton, with his theory of inclusive fitness (3). Hamilton illustrated that although to the observer helping behavior appears altruistic, from a genetic perspective it is a case of a gene in one individual helping to replicate an identical copy of itself in another individual. This concept, coined Hamilton's rule ($rb - c > 0$), demonstrated that altruism evolves when the gene copies an individual passes on by helping a breeder produce extra offspring (b: benefits), scaled by the probability that they share the gene for altruism (r: relatedness), outweighs the gene copies it loses by not producing its own offspring (c: costs) (3–5).

Hamilton's rule has played a highly influential role in explaining why cooperative breeding occurs. Painstaking, long-term studies of marked individuals over multiple generations have allowed proxies of rb and c to be estimated in many cooperative breeding species (1, 2). This has revealed that altruistic behavior almost always arises in family groups where mature offspring from previous breeding attempts remain with their parents to help raise siblings, to which they are highly related (7) (there are cases where multiple adults reproduce together that are often referred to as "cooperative breeding," but these can be explained by individuals increasing their own reproductive success, not that of others, so do not represent cases of

altruism). The benefits of such help to parents are often clear, allowing them to live longer and produce more offspring and the costs to helpers, although more difficult to accurately quantify, are often thought to be reduced by options for successful independent breeding typically being poor (1, 2, 8, 9). So the puzzle of helping behavior has largely been solved, or has it? In the vast majority of cooperatively breeding species only a proportion of individuals ever help, with others pursuing independent breeding opportunities from the get go (Fig. 1) (1, 2). Despite decades of research into why helpers help, empirical tests of why helper and nonhelper strategies stably coexist both within and between animal species have been lacking (Fig. 1), jeopardizing our ability to predict patterns of sociality.

In PNAS, Wang and Lu (6) address this issue, presenting a case study that explains why some individuals help while others do not. High up on the Tibetan plateau, Wang and Lu studied a small burrow-nesting bird, the Tibetan ground tit, *Pseudopodoces humilis* (Fig. 1). For 12 y, they monitored family relationships, patterns of parentage, and how many offspring were successfully raised by hundreds of individuals over an area of 5 km^2. They found, similar to many other cooperatively breeding birds, that around a quarter of the pairs were assisted by one or more adult male helpers that remained with their parents to help raise siblings, before departing to breed on their own. In the other three quarters of pairs, offspring left their parents as soon as possible, enabling them to get an extra year of breeding under their belt compared with those that helped.

Remarkably, across this 12-y period the relative frequency of helpers to nonhelpers was almost exactly the same, despite threefold differences in the percentage of pairs receiving help. It is generally assumed in such facultative cooperative breeders that all individuals are potential helpers and make a decision as to whether to help according to factors such as environmental conditions or mate availability (2, 10). Such a stable balance between helper and nonhelpers over periods where the frequency of cooperative breeding varies so much suggests that is not the case
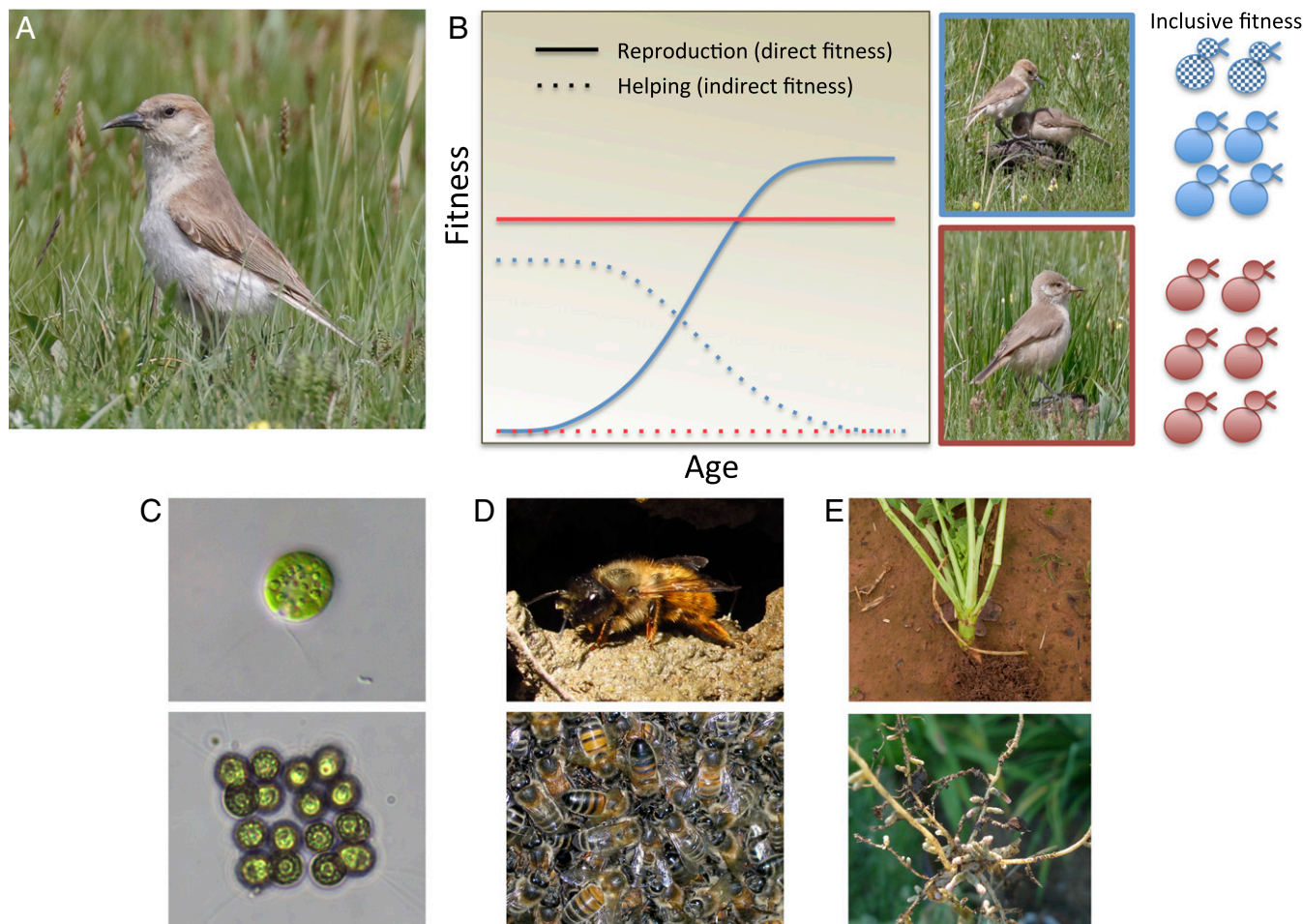
Fig. 1. The coexistence of helper and nonhelper strategies. (*A*) Tibetan ground tits, which were studied for 12 y by Wang and Lu (6), have nonreproductive helpers at around 25% of nests. Image courtesy of Flickr/Dave Curtis. (*B*) Individuals that help during the start of their lives ("helper morphs," blue) have equal fitness to those that never help ("nonhelper morphs," red) as a result of passing on their genes by helping relatives early in life (indirect fitness: dashed lines and symbols) and reproducing (direct fitness: solid lines and symbols) with the aid of helpers later in life. The coexistence of social and nonsocial forms is also widespread across closely related species in nature, and at all levels of life. Image courtesy of Flickr/Dave Curtis. (*C*) Multicellularity: unicellular forms, such as *Chalmydomonas* spp., coexist with multicellular forms, such as *Gonium*. (Magnification: 400×.) Images courtesy of Maria Svensson-Coelho (Lund University, Lund, Sweden). (*D*) Eusociality: solitary bees, such as *Osmia bicornis*, coexist with eusocial forms, such as *Apis mellifera*. (*Upper*) Image courtesy of Flickr/Nigel Jones. (*Lower*) Image courtesy of Flickr/Will George. (*E*) Symbioses: species that do not form nitrogen fixing symbioses, such as *Brassica napus*, often coexist with species that do such as *Pisum sativum* that house bacteria within root nodules. (*Upper*) Image courtesy of Flickr/CropShot. (*Lower*) Image courtesy of Flickr/sara'mer.

in this species. So what maintains the stable coexistence of helpers and nonhelpers in this system?

Wang and Lu (6) tested the possibility that helpers and nonhelpers are genetically determined strategies maintained in a constant balance through equal fitness returns (11, 12). Although Hamilton's rule has generally been applied in animals to understand when altruism evolves in a population (i.e., when $rb - c$ is greater than 0), in theory, stable equilibriums may occur in some populations with certain genotypes fulfilling this inequality, while for others rb is less than c, and so helping is not favored. For this to hold true, two conditions must be met. First, variation in the decision to help must have a genetic basis. Second, the inclusive fitness of helpers—that is, the number of gene copies they pass to subsequent generations via their own offspring plus those gained from helping relatives—must be equal to that acquired by nonhelper strategies. These are difficult pieces of evidence to gather. The genetic basis of helping has only been estimated once before in a cooperatively breeding vertebrate (13), and only approximate indications of the costs and benefits of helping are usually

obtained (2). Cooperative breeding birds are typically very long-lived (14), and so measures such as yearly breeding success are used as fitness proxies (2), but may poorly represent the lifetime fitness consequences of helping (15).

Wang and Lu (6) approached this challenge by examining the complete life histories of individuals to identify those that never helped and those that helped at some point during their life. This provides a robust basis for examining selection on helping behavior, as it avoids the pitfalls associated with focusing on what individuals do at a snapshot in time. Using the classification "ever helped" and "never helped" in conjunction with pedigrees that allow genetic and environmental sources of variation to be separated, the authors estimate that around 50% of variation in the likelihood of helping is explained by genetics. This is at the upper limit of estimates of genetic variation in behavioral traits in ecological studies (16), lending support for the first condition that helper and nonhelpers are genetically determined "morphs."

The second condition of equal fitness of helpers and nonhelpers required a few more calculations. Estimating the fitness of

nonhelpers was relatively straightforward and involved adding up the offspring produced by males, after checking and adjusting for a few cases where females had sneaked fertilizations with other males. In contrast, estimating the fitness of helpers was a bit more complicated. During the helper phase, fitness depends on the extra offspring individuals help raise, which was estimated as the difference between the number of chicks helped and nonhelped pairs fledged, multiplied by how related they are to those offspring. As females in this species are generally monogamous, helpers typically help full-siblings and so the fitness returns per extra offspring are almost equal to that gained from rearing their own offspring. Once males finish helping they attempt to breed on their own and the currency of fitness switches to direct reproduction. Although they start breeding later than nonhelpers, if they manage to survive more than a few breeding seasons, they reap the rewards of coming from a lineage of helpers, and their sons begin to help them, boosting their offspring production. So after the calculator had finished whirring and fitness during helping and breeding periods was summed, who was the winner, helpers or nonhelpers? Amazingly it was pretty much a dead heat, providing support for the second condition of equal fitness between the two strategies (Fig. 1).

The take-home message, facultative cooperative breeding at the population level may occur because $rb = c$, with some genotypes propagating genes purely through prioritizing their own reproduction ($rb < c$), while other genotypes gain a similar fitness through a combination of helping and direct reproduction ($rb > c$). It remains to be established how such helper and nonhelper morphs originate and what the underlying mechanisms are that makes obtaining fitness in different ways more or less advantageous. For example, in noncooperative breeding species, patterns of senescence frequently vary with some individuals investing in early-life reproduction at the expense of late-life performance, whereas others do the opposite (17). Could it be that helper strategies in facultative cooperative breeders originate as a way of late-life bloomers gaining an extra bit of fitness early in life before initiating their expensive reproductive physiology? Alternatively,

one can imagine a scenario where ancestral populations were composed entirely of helpers, but some genotypes have evolved physiological mechanisms that allow them to compete for independent reproductive opportunities earlier in life, abandoning the decision to help (18). The results presented by Wang and Lu (6) also raise questions about how helper and nonhelpers are maintained in frequency over time. A detailed examination of how the inclusive fitness of these two strategies vary in different background frequencies of cooperative breeding would be revealing, and examining helper decisions under manipulated conditions, such as breeder removals, would provide further experimental evidence of how helper and nonhelper genotypes are expressed under different social contexts. Undoubtedly, these fascinating findings will lead to a number of follow-up studies, not only in the Tibetan ground tits, but also more generally among cooperatively breeding vertebrates.

Playing devil's advocate, one might argue that this is just another study of cooperative breeding birds that demonstrates the benefits of helping versus not helping, which has been studied intensively over the last few decades (1, 2). However, this misses the broader point that requires greater attention. The evolution of life on earth has been characterized by individual replicating units cooperating to form higher levels of complexity, such as the major transitions to the eukaryotic cell, obligate multicellularity, and eusocial societies (Fig. 1) (19). The importance of such transitions is becoming increasingly recognized and the conditions that facilitate this are now a thriving area of research (20). Nevertheless, in most of the situations where these transitions have occurred, there are coexisting nonsocial forms that are prospering under similar conditions. If natural selection is continually finding optimal solutions to ecological problems, then how do we explain this? Wang and Lu's study (6) contributes to the empirical dialogue on this topic that will be important to extend beyond the realms of cooperative breeding to other levels of life. This will provide a more thorough understanding of why social and nonsocial strategies have evolved alongside each other and continue to coexist through the ongoing flux of the earth's biodiversity through time.

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