



# Hamilton's inclusive fitness maintains heritable altruism polymorphism through $rb = c$

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Edited by Joan E. Strassmann, Washington University in St. Louis, St. Louis, MO, and approved December 12, 2017 (received for review June 7, 2017)

**How can altruism evolve or be maintained in a selfish world? Hamilton's rule shows that the former process will occur when  $rb > c$ —the benefits to the recipients of an altruistic act  $b$ , weighted by the relatedness between the social partners  $r$ , exceed the costs to the altruists  $c$ —drives altruistic genotypes spreading against nonaltruistic ones. From this rule, we infer that altruistic genotypes will persist in a population by forming a stable heritable polymorphism with nonaltruistic genotypes if  $rb = c$  makes inclusive fitness of the two morphs equal. We test this prediction using the data of 12 years of study on a cooperatively breeding bird, the Tibetan ground tit *Pseudopodoces humilis*, where helping is performed by males only and kin-directed. Individual variation in ever acting as a helper was heritable ( $h^2 = 0.47$ ), and the resultant altruism polymorphism remained stable as indicated by low-level annual fluctuation of the percentage of helpers among all adult males (24–28%). Helpers' indirect fitness gains from increased lifetime reproductive success of related breeders statistically fully compensated for their lifetime direct fitness losses, suggesting that  $rb = c$  holds. While our work provides a fundamental support for Hamilton's idea, it highlights the equivalent inclusive fitness returns to altruists and nonaltruists mediated by  $rb = c$  as a theoretically and realistically important mechanism to maintain social polymorphism.**

cooperative breeding | Fisher's natural selection theorem | kin selection | lifetime fitness | quantitative genetics

The basis underlying Hamilton's rule  $rb > c$  lies in the gene's-eye view of evolution: natural selection will favor altruism over nonaltruism if the indirect fitness rewards to altruists  $rb$ , which result from copies of the genes passed indirectly via related social partners, more than offset the costs to them,  $c$ , which represent the loss of copies of the genes due to performing altruism (1). From a perspective of population genetics,  $c$  means the difference in direct fitness between altruistic and nonaltruistic genotypes. Therefore,  $rb > c$  typically describes a dynamic process during which adaptive altruistic genotypes keep increasing in frequency within a population against nonaltruistic genotypes. With its general ability and tractability to capture the essence of social evolution, Hamilton's rule has elicited a good deal of theoretical (2–9) and empirical (10) attention.

However, we emphasize that natural selection not only drives new, adaptive variants to replace old, less adaptive ones but also favors different variants to coexist stably. Thus, in addition to taking the dynamic state as specified by  $rb > c$ , altruistic genotypes may persist by forming a balanced behavioral polymorphism with nonaltruistic genotypes during the evolutionary tug-of-war between the two morphs, with the outcome depending on their relative fitness. Theoretically, the equilibrium between altruistic and nonaltruistic genotypes, or evolutionarily stable state (11), can be maintained by  $rb = c$ . This is because the equality implies that the indirect fitness benefits to individuals with altruistic genotype  $rb$  fully compensate for the direct fitness costs to them,  $c$ , permitting both morphs of the altruism polymorphism to have equal inclusive fitness so that they cannot invade each other (Fig. 1). The equivalent inclusive fitness mechanism for the maintenance of altruism

polymorphism through  $rb = c$  is consistent with Fisher's theorem of natural selection (12), which states that for a heritable trait to persist in an equilibrium population, it must cause no change in the population's average fitness. An allele-based mathematical simulation gave a similar prediction (13). Moreover, the mechanism of fitness equivalence has been found to act in holding some morphological polymorphisms (14, 15). In the light of the ubiquity of altruism polymorphisms in nature (*SI Appendix*), our theoretical prediction deserves empirical testing to understand how different social morphs to coexist within a population.

Here we test the prediction using a 12-y dataset of individual relationship and lifetime reproductive success from a population of the Tibetan ground tit *Pseudopodoces humilis* (16). As in most avian cooperative breeders, helping in this species is kin-directed. Extra-pair paternity occurs at a very low rate (0.5% of offspring), potentially promoting kin selection (17). Cooperative breeding is facultative in that some pairs (28% on average) in the population have helpers, which aid the breeders by defending territory and feeding nestlings. A helper usually helps for one breeding season and then it breeds itself ("ever giving help"), but in contrast, some breeding individuals have never helped during their lifetime ("never giving help"). On the other side of the coin, some breeders have ever received help ("ever receiving help"), whereas the others have not ("never receiving help"). No individual has been found to adopt a floating strategy.

## Results

To produce a robust test, we must first verify that variation in performing altruism among individuals within the study population is heritable. This is because heritability underlies the basis of defining ever and never giving help as two alternative

### Significance

**Why should some individuals help others at the expense of their own fitness? Hamilton's elegant formula  $rb > c$  resolves the major paradox in social evolution and has become a golden rule of sociobiology. However,  $rb > c$  only tells part of the story, namely how altruistic genotypes expand. Theoretically, altruistic genotypes can persist by coexisting stably with nonaltruistic ones relying on  $rb = c$ , which may let both genotypes have equal inclusive fitness. We present evidence for this prediction using long-term data on a species of bird. Our work suggests that altruism should be understood beyond  $rb > c$ , given that  $rb = c$  has the potential to explain widespread altruism polymorphisms in nature.**

Author contributions: X.L. designed research; C.W. and X.L. developed critical ideas; C.W. performed research; C.W. analyzed data; and X.L. wrote the paper.

The authors declare no conflict of interest.

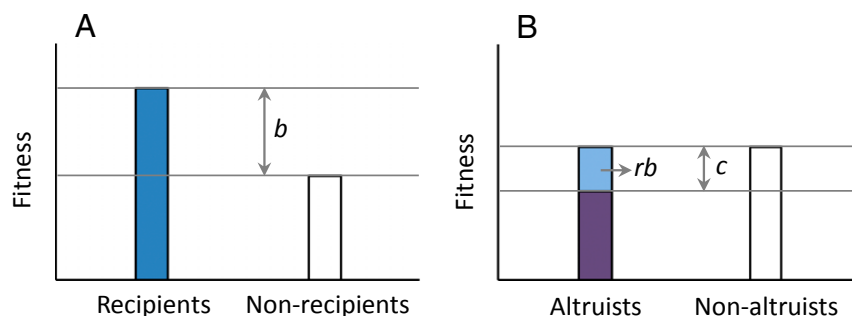
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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1710215115/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1710215115/-DCSupplemental).



**Fig. 1.** A sketch showing the testing system for the equivalent inclusive fitness mechanism mediated by  $rb = c$  to maintain altruism polymorphism. (A) Altruism enhances lifetime direct fitness of the recipients, where  $b$  is the direct fitness difference between recipients and nonrecipients. (B) The indirect fitness payoffs for altruists  $rb$  (where  $r$  is the genetic relatedness between altruists and recipients) perfectly compensate  $c$ —the lifetime direct fitness losses suffered by altruists relative to nonaltruists.

phenotypes (the family lineages carrying either altruistic or nonaltruistic genes), which constitute a genetic polymorphism for natural selection to operate on. Specifically, an unambiguous definition of the two phenotypes makes it justified to evaluate lifetime inclusive fitness of ever-giving-help ground tits, even though they subsequently died or bred themselves. In fact, Hamilton's theory of inclusive fitness is established on quantitative genetics (1–3, 8). Previous attempts to test this theory, including those to parameterize Hamilton's rule, however, failed to set altruism heritability as a necessary prerequisite (10).

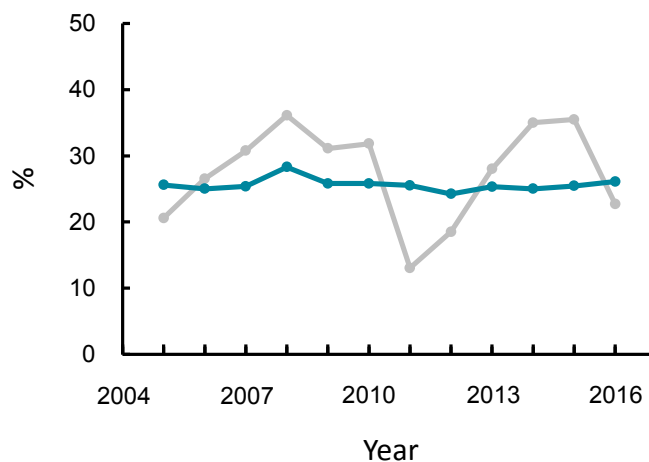
Using the pedigree-based threshold animal model, we demonstrated a significant genetic component of individual variation in ever vs. never being a helper in the ground tit population, with the estimated narrow-sense heritability ( $h^2$ ) being 0.47 (95% CI: 0.16–0.75). To our knowledge, this is the second estimate for heritability of altruistic behavior in natural populations. The first estimate was made for the Western bluebird *Sialia mexicana* (18), reporting a significant result ( $h^2 = 0.76$ ). Nevertheless, that analysis was based on a dataset with an unbalanced sample size of helped vs. unhelped nests (22 vs. 251) and without excluding the relatively high rate of extra-pair paternity (17% of offspring).

An equilibrium state of altruism polymorphism is the indicator by which we may predict that  $rb = c$  is going on. In this ground tit population, the percentages of helpers among all adult males annually varied between 24.2% and 28.3% (mean  $\pm$  SD:  $25.6 \pm 1.0\%$ ; 3.9% for the coefficient of variation) over the 12-y study period, although the percentages of helped nests fluctuated extensively, between 13.0% and 36.1% ( $27.5 \pm 7.4\%$ ; 26.9% for the coefficient of variation) (Fig. 2). The very low temporal variability in the relative number of helpers within the population suggests that altruistic and nonaltruistic genotypes could be at an almost stable equilibrium.

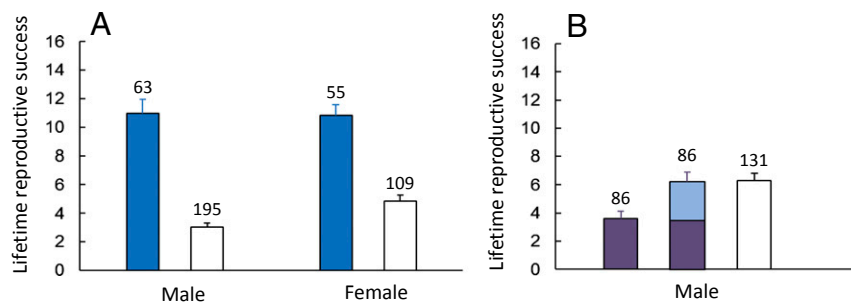
We then examined helping's fitness benefits to the recipients and its fitness costs to the helpers. The general linear mixed-model analysis found that controlling for territory quality and year of birth, ever-receiving-help males had significantly higher lifetime reproductive success than never-receiving-help males ( $t = 10.35$ ,  $df = 253.85$ ,  $P < 0.001$ ); this was also the case when comparing lifetime reproductive success between ever- and never-receiving-help females ( $t = 6.85$ ,  $df = 159.83$ ,  $P < 0.001$ ; Fig. 3A). On the other hand, with all else being equal, the lifetime direct reproductive success of ever-giving-help males was significantly lower than that of never-giving-help ones, an indication that helping was costly (Fig. 3B and Table 1). Given that helpers enhanced recipients' lifetime reproductive success at the expense of their own direct fitness, helping in the ground tits was altruistic.

Alternatively, the observed significant difference in lifetime fitness between ever- and never-receiving-help breeders might be due to differential reproductive potential of the two groups of

breeders rather than helpers' contribution. However, that should not be the case. There were statistically significant differences between ever- and never-receiving-help breeders in body mass based on a  $t$  test (male:  $t = 1.01$ ,  $df = 213$ ,  $P = 0.31$ ,  $BF_{01} = 3.78$ ; female:  $t = 0.64$ ,  $df = 128$ ,  $P = 0.52$ ,  $BF_{01} = 4.36$ ) and tarsus length (male:  $t = 1.13$ ,  $df = 213$ ,  $P = 0.26$ ,  $BF_{01} = 3.36$ ; female:  $t = 1.27$ ,  $df = 128$ ,  $P = 0.21$ ,  $BF_{01} = 4.84$ ), the two commonly used indicators of individual quality (19). Furthermore, our earlier study of the ground tit population found that for a brood reared by a breeding pair plus a helper, the helper contributed to approximately one-third of the total amount of food delivered to the brood. The helped breeders of both sexes expended a significantly lower provisioning effort than the breeders that held no helper, more likely as a response to the presence of the helpers (20). This was supported by a within-individual comparison, which revealed that provisioning efforts on each nestling were 40% in males and 25% in females ( $n = 6$  breeding pairs) lower when they were helped than when they were not. The reduced parental investment should be responsible for the higher annual survival rates and longer longevities of ever-receiving-help breeders (21), and thus the greater lifetime reproductive success as shown here. One might also argue that the lower lifetime direct reproductive success of ever-giving-help males could not be due to helping but because these males were lower quality relative to never-giving-help males. However, the lack of difference in body mass ( $t = 1.06$ ,  $df = 175$ ,  $P = 0.29$ ,  $BF_{01} = 5.30$ )



**Fig. 2.** Yearly variation in the percentages of helpers (blue line) among all adult males and of helped nests (gray line) among all nests in the Tibetan ground tit population across the study period.



**Fig. 3.** Comparisons of lifetime fitness between individual ground tits to test the prediction that equivalent inclusive fitness mediated by  $rb = c$  maintains altruism polymorphism. (A) Lifetime reproductive success of ever-receiving-help (blue columns) vs. never-receiving-help (white columns) breeders. (B) Lifetime direct reproductive success of ever-giving-help (purple columns) vs. never-giving-help (white column) males, and indirect fitness benefits of ever-giving-help males (light blue column). Values are given as mean + SE, with sample sizes above the SE bar.

and tarsus length ( $t = 0.68$ ,  $df = 176$ ,  $P = 0.50$ ,  $BF_{01} = 5.71$ ) between the two groups of males does not support the assumption.

Having verified that costly helping enhanced the recipients' fitness, we next investigated whether the indirect fitness benefits gained by ever-giving-help male ground tits, equaled their lifetime fitness costs,  $c$ . The general linear mixed-model analysis based on Price's quantitative genetic idea of kin interaction (2) yielded a large  $P$  value, 0.78 (Table 1), suggesting a high probability of accepting the null hypothesis: the inclusive fitness benefits of ever-giving-help males, measured as their lifetime direct reproductive success plus their indirect fitness benefits, did not differ from the personal lifetime reproductive success of never-giving-help males (Fig. 3B). This conclusion was reinforced by the small correlation coefficient of determination ( $R^2 = 0.002$ ) for a single-predictor general linear mixed model, which indicated that whether to be a helper almost had no effect on individual variation in inclusive fitness. Actually, the difference in mean inclusive fitness between the two groups of males was slight (0.04 or 0.6%; Fig. 3B). The very low statistical power (0.05 for a two-tailed test) of the current analysis seemed not to support the conclusion. However, this indicator has been considered useless when effect size is very small (22), such as in our case. A Bayes factor approach further provided strong evidence in favor of our prediction, with  $BF_{01} = 24.59$  indicating that the data were almost 25 times more likely under the null hypothesis than under the alternative hypothesis (23, 24). Together, these lines of evidence can lead to the conclusion that  $rb = c$  was statistically valid and the equivalent inclusive fitness mechanism may selectively maintain the heritable altruism polymorphism in the ground tit population.

## Discussion

A major implication of our work is to offer a fundamental support for Hamilton's theory of inclusive fitness (1), a critical concept in the textbooks of evolutionary biology and sociobiology

**Table 1.** Results of general linear mixed-model analyses to assess whether helping behavior affected lifetime reproductive success of male ground tits ( $n = 217$  birds), with territory quality as a covariate variable and year of birth as a random variable

| Model                              | Coefficient ± SE | $t$  | $df$   | $P$   |
|------------------------------------|------------------|------|--------|-------|
| Without including indirect fitness |                  |      |        |       |
| Ever or never giving help          | 2.69 ± 0.80      | 3.33 | 208.82 | 0.001 |
| Territory quality                  | 0.36 ± 0.32      | 1.08 | 209.00 | 0.28  |
| Including indirect fitness         |                  |      |        |       |
| Ever or never giving help          | 0.24 ± 0.83      | 0.28 | 208.94 | 0.78  |
| Territory quality                  | 0.55 ± 0.34      | 1.60 | 208.37 | 0.12  |

but the focus of controversy, especially during recent years (25, 26). The evidence of altruism heritability is consistent with the core premise of Hamilton's theory: altruistic behavior can evolve through kin selection depending on a genetic component (1–3, 8). Our empirical demonstration of  $rb = c$ , which is deduced from Hamilton's rule, not only uncovers the role of indirect benefits in favoring altruism but also confirms the validity of  $rb > c$ , with which Hamilton formulated his theory of inclusive fitness. Importantly, our approach is robust because it follows the rigorous program of testing the theory of inclusive fitness, which demands a strict definition of altruism, the heritability of altruism as the basis for kin selection to act on, lifetime fitness to measure  $b$  and  $c$ , and quantitative genetic models to compare inclusive fitness (4–6, 27). As far as we know, our work is the first to test this theory taking such a program.

Of more general importance, our work may inspire researchers to understand the evolution of altruism beyond  $rb > c$  in both theory and practice. With  $rb = c$  as a balancing state between altruistic and nonaltruistic genotypes, either of the genotypes may spread when  $rb > c$  or  $rb < c$  occurs. The framework constituted by the three equations about the evolution of altruism may be theoretically interpreted with reproductive altruism. The mechanism mediated by  $rb = c$  should operate in facultatively cooperative breeding animals (*SI Appendix*), given that theory suggests that extant traits including altruism should have been fixed after experiencing directional selection (28). Eusociality in which lifetime sterile workers are present in all colonies in a population persists as  $rb > c$  has pushed altruistic genotypes to go to fixation, whereas solitary breeding results when nonaltruistic genotypes have taken over the population relying on  $rb < c$ . Dynamic changes in the two genotypes in frequency may be understood by the fact that the origin and loss of solitary, facultatively cooperative, and eusocial lifestyles repeatedly occur across phylogenies (29, 30), and that these social forms shift within a single species across environments (ref. 31 and *SI Appendix*). Therefore, the framework based on  $rb$  vs.  $c$  relations has potential as a predictive and analytical tool to explore the evolutionary transition of social systems. Such explorations can be conducted with reproductive altruism systems by quantifying  $r$ ,  $b$ , and  $c$  in association with kin structure and demography in different ecological regimes. It is also helpful for evaluating the evolution of social interactions beyond reproductive altruism, including those between nonkin (32), where  $r$ ,  $b$ , and  $c$  could all be positive, negative, or zero (33).

Bearing the framework for the evolution of altruism in mind is particularly important to empirical research where Hamilton's  $rb > c$  has overwhelming influence. Indeed, previous studies attempted to test  $rb > c$  using the systems with an altruism polymorphism (10); there could have been a publication bias against the results inconsistent with the inequality (34). More

unfortunately, almost all of these authors did not compare  $rb$  and  $c$  statistically but instead did so with their simple arithmetic means (10), which could hardly lead to any convincing conclusion. Employing these case studies, we may find evidence for our argument by treating the outcomes based on arithmetic means as a set of random samples from a population with an altruism polymorphism. As expected, there is no greater probability of observing  $rb > c$  than  $rb < c$  (8 vs. 5,  $\chi^2 = 0.69$ ,  $df = 1$ ,  $P = 0.41$ ), regardless of the potential publication bias favoring the former (34).

In terms of alternative reproductive strategies (35), our work elaborates a kin selection-based form by demonstrating the heritability of altruism and clarifying the mechanism underlying the maintenance of individual variation in performing altruism. Specifically, while altruism polymorphism here is defined on a between-individual, lifetime basis, the altruistic behavior occurs in a within-individual, age-dependent way. In the study population, some ground tits forgo their first-year reproduction and help kin to accrue indirect fitness benefits; then they, if they survive, gain direct fitness benefits by breeding themselves. As a consequence, these ever-giving-help individuals can ultimately achieve the same lifetime inclusive fitness as those never-giving-help individuals. It is worth noting that helping could bring helpers some direct benefits, which can subsequently contribute to improving their personal reproductive success. In our study system, however, helpers seemed not to pursue such benefits through inheriting natal territory (36% of 36 vs. 40% of 131;  $\chi^2 = 0.15$ ,  $df = 1$ ,  $P = 0.70$ ). Nevertheless, other direct benefits from helping, such as acquiring breeding experience (36), remain to be investigated.

There are alternative explanations for how the altruism polymorphism evolutionarily remains. One way this could occur is that altruistic alleles, if deleterious, can maintain a stable equilibrium frequency when they are eliminated by selection but are constantly reintroduced by mutation (37). The selection-mutation balance mechanism is less likely to work in the ground tit social system, where altruistic genotypes always have the same inclusive fitness as nonaltruistic genotypes so that selection against altruism should not have taken place. Also, negative frequency-dependent selection favoring rarer genotypes can allow a population to harbor both altruistic and nonaltruistic morphs (38). Almost unchangeable annual proportions of helpers relative to all adult males suggest a nearly stable altruism polymorphism, at least during the study period, excluding the mechanism of frequency-dependent selection. Even though the relative frequencies of altruistic genotypes fluctuate under frequency-dependent selection, the mean inclusive fitness of the two morphs should be statistically equal (i.e.,  $rb = c$ ) in the long run. Additionally, the lack of significant difference in body mass and tarsus length between ever- and never-giving-help males suggests that the maintenance of altruism polymorphism less likely depended on individual quality (19), which may indicate the competitiveness for access to territory or mate, the major ecological constraints on independent reproduction in birds (39). More indicators such as social dominance and immune level remain to be examined to explore whether the altruistic strategy is status dependent (40).

## Materials and Methods

**Study System.** Data were collected during 2005–2016 from an individually banded ground tit population composed of 30–50 pairs within a 480-ha study plot (30°28'N, 91°05' E, 4,300 m above sea level) in Dangxiong County, south Tibet. Life history and social organization of this population have been described in detail elsewhere (16). Here we briefly outline the main features.

Ground tits live in all-purpose territories year-round. Within territories, they construct one burrow for nesting and another for roosting during the nonbreeding period, which are a 0.8–2.9-m straight tunnel with a chamber at the end (41). During the nonbreeding period, the birds form family groups that contain male and female parents, philopatric young, and immigrants.

When breeding, groups break into socially monogamous pairs, some of which have helpers. A pair usually produces one clutch per year, with a clutch size of 4–9 eggs and a brood size at fledging of 1–9 young. Incubation is undertaken by females only, lasting 15–16 d; nestlings are fed by both parents and helpers, if any, for 24–26 d. Natal dispersal is usually limited to less than five territories, and female juveniles move far more than male juveniles.

Apparent annual survival rates of breeding males, breeding females, and helpers are 51%, 49%, and 43%, respectively. Pair bonds remain unless one partner dies, and only 0.5% divorce. Annual recruitment rates are 20% in male fledglings and 11% in female fledglings. Almost half (49%) of the yearling males breed independently and the other (51%) become helpers. Longevity of individuals who survive across at least one winter averages 1.9 (1–9) y in males and 1.7 (1–7) y in females. Incest and extra-pair parentage both are rare: 1% of broods in the former and 3% in the latter.

A helped pair has one (85%) or two to three helpers (15%). Helpers all consist of males, the majority of which are yearlings (83%) and the minority older individuals (17%). Helping is kin-directed, toward both (62%) or one (20%) of the parents, as well as other first- or second-order relatives (18%). Most helpers help only once during their lives (90%), and a few do so for two or three breeding seasons (10%); then they breed on their own if they survive.

**Field and Laboratory Methods.** We captured adult ground tits by placing a 1 × 1-m mist net around the entrance of nesting burrows and banded them with colored plastic and numbered metal leg rings. We checked nest contents and banded nestlings by digging a vertical shaft next to the nest chamber (the shaft was then plugged). Every winter, we banded immigrants by capturing them in roosting burrows. Social organization per nest was determined by observing behaviors of banded individuals. A blood sample of 10–30  $\mu$ L was collected from each banded individual to determine its sex (supplemented by evidence from behavior and presence/absence of an incubation patch in adults) and genetic identity by means of molecular biology techniques (42, 43).

**Territory Quality Evaluation.** We marked all nest sites located per year on a map of the study plot and determined the annual territory of each breeding pair as the areas enclosed by the midperpendicular of the connecting lines between neighboring nests. All annual territories in the plot over the study years were put together, and the maximal overlapped section around a nest was defined as a permanent territory. A total of 91 permanent territories that involved 551 nests were identified. The quality of a permanent territory was evaluated with the mean annual fledgling production by all of the pairs breeding within the territory over the study years.

**Heritability Estimate.** A pedigree was established with 592 individuals (335 males and 257 females) who were engaged in at least one breeding event (bred independently or helped). Extra-pair parentage was taken into account when constructing the pedigree (only 1 out of the 592 individuals was sired by a male outside the study population). Birds that immigrated into the study area were assumed to be yearlings and unrelated to each other or to local individuals. Based on the pedigree, we estimated the heritability of helping behavior with a threshold animal model (44, 45), in which the binary response variable was specified as 1 for ever giving help or 0 for never giving help, with sex as a fixed factor. Analyses were conducted using the MCMCglmm package (46) implemented in R version 3.2.5 (47). A parameter-expanded prior ( $V = 1$ ,  $\nu = 1,000$ ,  $\alpha, \mu = 0$ ,  $\alpha, V = 1$ ) was set for the random effect. The binomial model with probit link was run with 16,000,000 iterations, 100,000 burn-in, and thinning of 3,000, to allow the simulations to converge adequately with weak autocorrelation (<0.03), large effective size (>5,000), and well-performed chains (46).

Individual variation in acting as a helper might be a consequence that cooperative breeding depends on territory quality and high-quality territories tend to be inherited within family groups. We excluded the probability because the quality of a territory did not predict whether the territory held helpers (a generalized linear mixed-model analysis with year as the random variable:  $z = 1.32$ ,  $df = 471.40$ ,  $P = 0.19$ ,  $BF_{01} = 7.80$ ).

**Fitness Measure.** According to the definition of altruism in the context of inclusive fitness theory (4–6),  $b$  and  $c$  should be measured with lifetime direct fitness. The most appropriate proxy of lifetime fitness has been considered to be lifetime reproductive success (LRS), the total number of fledglings produced by an individual over its life, because it combines several critical components of fitness, including mating success, annual offspring productivity, survival, and longevity (48). In this study, the data were available for 422 individuals, which were banded as fledglings, bred, or helped at least

once. Indirect fitness benefit (*IF*) gained by an ever-giving-help individual was calculated using the following equation:

$$IF = r_{\text{male}}(LRS_{\text{helped male}} - \text{mean } LRS_{\text{male}}) + r_{\text{female}}(LRS_{\text{helped female}} - \text{mean } LRS_{\text{female}})$$

where  $LRS_{\text{helped male}}$  and  $LRS_{\text{helped female}}$  represent *LRS* of male and female breeders with whom the focal individual ever helped, respectively; mean  $LRS_{\text{male}}$  and mean  $LRS_{\text{female}}$  represent the average of *LRS* of all male and female individuals in the population, respectively;  $r_{\text{male}}$  and  $r_{\text{female}}$  represent the relatedness between the focal individual and the recipients, which were determined based on the pedigree. In a few cases where a breeder was helped by more than one helper, the increased direct fitness benefits from helping were equally divided to each helper. On occasion where a helper ever helped more than one nest in different years, we calculated the indirect fitness benefits to the helpers taking into account the increased direct fitness benefits to all of the involved breeders.

**Comparing Fitness.** General linear mixed models were employed to compare the differences in lifetime reproductive success between ever- and never-receiving-help individuals for each sex. The same procedure was performed

to compare the fitness differences between ever- and never-giving-help males, without and with including indirect fitness. Territory quality was assigned as a covariate variable and year of birth (the year in which an individual fledged) as a random variable to control for their potential effect on reproductive success. The inclusion of the two variables was less likely to lead to multicollinearity, because both of them, as was shown above, were unrelated to cooperative breeding. For all analyses, values of  $P < 0.05$  were considered to be statistically significant. We also provided Bayes factors (with default mixture-of-variance priors) as an alternative approach for statistical inference when  $P > 0.05$ , with  $BF_{01} = 3-20$  indicating a positive and  $BF_{01} = 20-150$  strong support for the null hypothesis (23, 24).

**ACKNOWLEDGMENTS.** We thank D. Ke, T. Yu, S. Tang, G. Zhang, Q. Zhao, H. Fan, W. Guo, Z. Li, and 16 other graduate students and W. Guan and five other volunteers for assistance in the field and laboratory. We thank S. Shen, Y. Tao, A. P. Møller, J. A. R. Marshall, L. Keller, S. A. West, D. C. Queller, A. F. G. Bourke, and X. H. Li for advice in preparing the manuscript; and D. W. Mock and three anonymous referees for comments on earlier versions of this manuscript. This research was supported by the National Natural Science Foundation of China (Grants 30425036, 30670337, 30830019, and 31572274).

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