



Altruism and natural selection in a variable environment

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Hamilton's rule provides the cornerstone for our understanding of the evolution of all forms of social behavior, from altruism to spite, across all organisms, from viruses to humans. In contrast to the standard prediction from Hamilton's rule, recent studies have suggested that altruistic helping can be favored even if it does not benefit relatives, as long as it decreases the environmentally induced variance of their reproductive success ("altruistic bet-hedging"). However, previous predictions both rely on an approximation and focus on variance-reducing helping behaviors. We derived a version of Hamilton's rule that fully captures environmental variability. This shows that decreasing (or increasing) the variance in the absolute reproductive success of relatives does not have a consistent effect—it can either favor or disfavor the evolution of helping. We then empirically quantified the effect of helping on the variance in reproductive success across 15 species of cooperatively breeding birds. We found that a) helping did not consistently decrease the variance of reproductive success and often increased it, and b) the mean benefits of helping across environments consistently outweighed other variability components of reproductive success. Altogether, our theoretical and empirical results suggest that the effects of helping on the variability components of reproductive success have not played a consistent or strong role in favoring helping.

social evolution | kin selection | cooperative breeding | bet-hedging

Hamilton's rule has been used to explain the evolution of a range of social behaviors, including altruism, selfishness, and spite, across the whole tree of life (1–8). This rule states that a trait will be favored if $rb - c > 0$, where c and b are the trait's effects on the actor and the recipient's relative reproductive success (fitness), respectively, and r is the genetic relatedness between social partners (1). This rule provides a simple way to explain why a social behavior is favored and why differences in behavior occur, both between species and between individuals within species (3, 5, 8–12). For example, it explains why cooperative breeding has evolved in only certain bird species (7, 13), why eusocial insects have sterile worker castes (14–16), and why bacteria kill themselves to release toxins (17). In all these cases, the advantage of Hamilton's rule is that it focuses on a small number of key factors that affect the costs and benefits of performing a behavior in a relatively simple way.

Recent work expanded Hamilton's rule to understand the evolution of social behaviors when individuals experience variable environments (18–20). This is potentially important because variable environments are the norm for most organisms, and cooperation may play a role in mitigating the effects of environmental variation (21–24). These studies focused on a scenario where the effect of a social trait on fitness could fluctuate between different environmental states. Behaviors that reduce variance in the absolute reproductive success of the actor and/or recipient across environments are usually predicted to be favored by natural selection, even if these behaviors have a net negative effect on average fitness (18, 25). Given the widespread use of Hamilton's rule and the ubiquity of environmental variation in the natural world, these theoretical results could revolutionize our understanding of social behaviors.

However, several questions remain. First, previous theoretical work has focused on how selection can favor behaviors that reduce the variance in fitness across environmental states (18, 25–28). Is a reduction in fitness variance always beneficial for the evolution of helping behaviors? Can selection also favor costly behaviors that increase the variance in fitness of recipients, as has been suggested for nonsocial behaviors (29)? Second, previous theory has usually relied on an approximation to generate easily interpretable biological predictions (18, 25–27, 30, 31). This approximation assumes that the variation in fitness across environments is small, in a way that could have led to biased conclusions. How often does this approximation predict selection in the wrong direction? Can an unapproximated Hamilton's rule generate easily interpretable predictions? Finally, empirical data are required to test the relative importance of mean versus variability effects on reproductive success in the evolution of altruistic helping

Significance

Evolutionary theory predicts that natural selection usually favors strategies that lower the variance in reproductive success in unpredictable environments. As environmental variability is often linked to sociality, recent theory suggested that selection can favor helping behaviors that lower the reproductive variance of relatives. We show that decreasing the reproductive variance of relatives can either favor or disfavor helping. We then examined the reproductive success in 15 species of cooperatively breeding birds. We found that i) helping did not consistently reduce reproductive variance, and ii) the mean benefits of helping generally outweighed other variability components of reproductive success, suggesting that the effect of helping on variability in reproductive success has not played a significant role in the evolution of helping.

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behaviors (23, 24, 32–38). How often do helping behaviors reduce the variance in fitness in nature? How important are the influences of helping on all fitness effects that are not captured by the mean?

We first derive Hamilton's rule for a variable environment without approximating expected relative fitness. Our model allows us to examine whether reducing the variance in fitness of relatives can be selected against and whether selection can also favor costly behaviors that increase the variance in fitness of relatives. We then examine the importance of environmental variation on the benefits of helping behaviors empirically. If helping behaviors are favored because they reduce the variance in fitness of relatives, then we would expect to observe this pattern empirically in natural populations. We tested this prediction by examining how helping influences variance in the reproductive success of breeders in 15 species (17 populations) of cooperative breeding birds. Finally, we used data from these species to parameterize the benefit terms in our version of Hamilton's rule. This allows us to estimate the relative extent to which helping is favored because it either increases mean reproductive success or reduces the variation in reproductive success.

Model

We first derive Hamilton's rule for a variable environment. Although an "unapproximated" condition for selection has been previously derived (18, 19, 25, 29), it does not provide easily interpretable biological predictions. Hence, previous predictions have mainly been based on an approximated equation for relative fitness, which takes the first few statistical moments of a Taylor series on the absolute reproductive success distribution across environmental states (mean and variance), discarding higher moments such as skew and kurtosis (18, 25, 30, 31). This approximation assumes that the very variation effects it aims to capture are small or absent (variation in fitness across environments is small). If higher-order moments influence selection, then the approximated version of Hamilton's rule could have led to biased results (29).

Hamilton's Rule in a Variable Environment. To remove the potential for such biases, our model does not approximate expected relative fitness. We consider a social trait p that affects the absolute reproductive success (absolute fitness) of the actor and that of its social partners. We assume that the population, with a given (fixed) genetical profile, can fluctuate between different environmental states $\pi \in \Pi$. Hence, across environmental states the social trait may have different fitness consequences, and the population average absolute reproductive success may also vary. Throughout, we mainly focus on between-generation (temporal) stochasticity so that all individuals are exposed to the same environmental state in each generation. We do not consider within-generation (demographic) stochasticity, where different individuals experience different environments at the same time [although our approach can be applied to demographic stochasticity as well; (18)]. Our starting point is the prospective Price's equation (29), which expresses the expected change in population average genetic value over a single generation that is attributable to selection [first term in the Price equation; (39)]. This expected change is taken over environmental states and is given by the expected covariance between genetic value and relative fitness across these states (29, 39, 40). Then, following Kennedy et al. and Queller's inclusive fitness partition method (10, 41, 42), we show in *SI Appendix, Appendix A1* that the social trait is favored when

$$\underbrace{-c_\mu + rb_\mu}_{\text{means-based Hamilton's rule}} + \underbrace{\nu\rho_E\sigma_{IF}}_{\text{volatility effects}} > 0. \quad [1]$$

Inequality (1) is a version of Hamilton's rule for variable environments which is not approximated and interpretable, compared to the previous approximated version based on the prospective Price equation (18). This expression gives the condition for when a trait is expected to increase in frequency from one generation to the next, rather than a condition for its long-term fate (e.g., fixation probability). The first part of the left-hand side of this inequality represents the classic means-based version of Hamilton's rule that is often applied empirically (8). The means-based Hamilton's rule focuses on the trait's arithmetic mean consequences for absolute reproductive success across environmental states (18). The terms c_μ and b_μ represent the trait's average absolute reproductive success cost to the actor and benefit to recipients, respectively, across environmental states, and r is the coefficient of relatedness between social partners (assuming constant r across environmental states). The second part of this inequality represents the influence of environmental variation, which we refer to as the trait's "volatility effects."

The volatility effects consist of three multiplicative, nonindependent components: ν , ρ_E , and σ_{IF} (Fig. 1). The coefficient of variation ν measures the variation in the inverse of population average absolute reproductive success across environmental states ($\nu = \text{std}(1/\bar{w}(\pi))/\mathbb{E}_\pi[1/\bar{w}(\pi)]$, where $\bar{w}(\pi)$ is the population average absolute reproductive success in environmental state π ; Fig. 1A). The coefficient ρ_E is the correlation across environmental states between the inverse of population average absolute reproductive success ($1/\bar{w}(\pi)$) and the inclusive fitness effect $-c_{(\pi)} + rb_{(\pi)}$. The terms $c_{(\pi)}$ and $b_{(\pi)}$ are the social trait's cost to the actor and benefit to recipients, respectively, in a given environmental state π (Fig. 1B). The correlation ρ_E is a measure of how the trait's net effects on fitness correlate with the inverse of population average absolute reproductive success. The last term in the volatility effect is the SD in inclusive fitness effects ($\sigma_{IF} = \text{std}(-c_{(\pi)} + rb_{(\pi)})$; Fig. 1C), which measures the variation in the traits' net effects on fitness across environmental states.

Our Hamilton's rule (Inequality 1) shows that even when the means-based Hamilton's rule is not met ($-c_\mu + rb_\mu \leq 0$), altruism can still be favored, if the consequences of environmental variation are both positive and sufficiently large ($\nu\rho_E\sigma_{IF} > 0$). This requires two conditions. First, altruistic helping leads to higher inclusive fitness benefits in environmental states where the inverse of population average absolute reproductive success ($1/\bar{w}(\pi)$) is higher ($\rho_E > 0$; This is often equivalent with higher inclusive fitness occurring in states where population average fitness is low, but not necessarily, as shown in *SI Appendix, Fig. S1*). Second, all three of the volatility factors must be non-negligible (the coefficient of environmental variation, ν , as in ref. 18; the fitness–environment correlation coefficient, ρ_E ; and the SD in inclusive fitness effects, σ_{IF} ; Fig. 1 and *SI Appendix, Figs. S1 and S2*). Hence, behaviors with zero mean effects ($c_\mu = b_\mu = 0$) can be favored as long as the volatility effects are positive, as previously shown (18). The advantages of decomposing volatility effects in this way are that each term (ν , ρ_E , and σ_{IF}) can be measured by empiricists and that they each provide some insight into when the total volatility effects would be negligible. If empiricists only have data on either costs or benefits, the term $\rho_E\sigma_{IF}$ can be further decomposed to isolate the volatility effects in costs and the volatility effects in benefits (see below; *SI Appendix, Appendix B*).

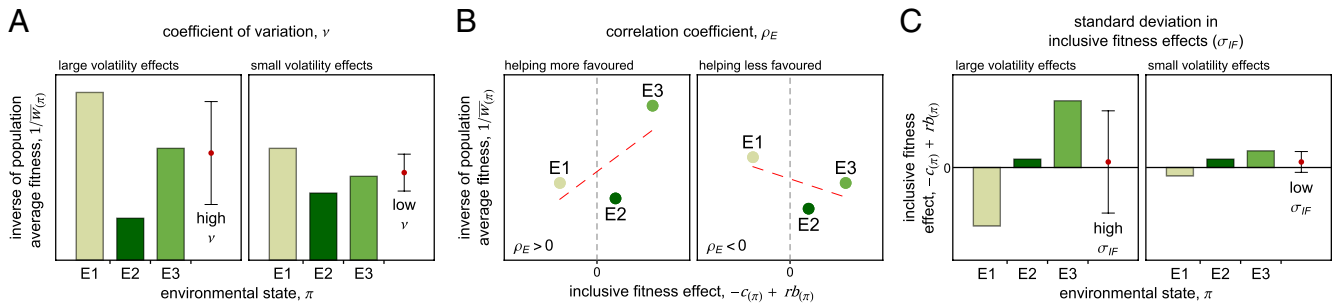


Fig. 1. Environmental variation and the direction of natural selection. The different panels examine the consequences of variation across three environmental states (π) for the volatility effect of inequality (1). (A) The coefficient of variation (ν) measures the variation in the inverse of the population average absolute fitness ($1/\bar{w}_{(\pi)}$) across the environmental states. A high variation in $1/\bar{w}_{(\pi)}$ increases the coefficient of variation ν , and in turn the influence of volatility effects on selection (Left), compared to a low ν (Right). (B) The coefficient ρ_E is the correlation across environmental states between the inverse of population average absolute fitness ($1/\bar{w}_{(\pi)}$) and the inclusive fitness effect ($-c_{(\pi)} + rb_{(\pi)}$). If larger inclusive fitness effects occur in environmental states where the inverse of population average fitness is higher, then ρ_E is positive, and helping is favored (Left). If larger inclusive fitness effects occur in environmental states where the inverse of population average fitness is lower, then ρ_E is negative, and helping is disfavored (Right). (C) The SD in inclusive fitness effects (σ_{IF}) measures the variation in the inclusive fitness effect across environmental states [$\sigma_{IF} = \text{std}(-c_{(\pi)} + rb_{(\pi)})$]. A high SD in inclusive fitness effects (σ_{IF}) increases the influence of volatility effects on selection (Left), whereas a low σ_{IF} decreases it (Right). We focus our discussion on helping, but the same patterns would hold for any form of social trait.

Environmental Variation and Selection for Altruism. Our Hamilton's rule predicts that reducing the variance in absolute reproductive success of relatives does not consistently favor altruism (Fig. 2). Under certain conditions, reducing the variance in fitness of relatives can favor altruism (when the correlation $\rho_E > 0$; Fig. 2B),

but it can also lead to the opposite and disfavor altruism (when $\rho_E < 0$; Fig. 2C and *SI Appendix, Fig. S3*). While reducing the variance in fitness is usually viewed as providing a benefit (18, 25), we find that can also be viewed as a cost, since it can be selected against even when it is personally beneficial (*SI Appendix, Fig. S4D*).

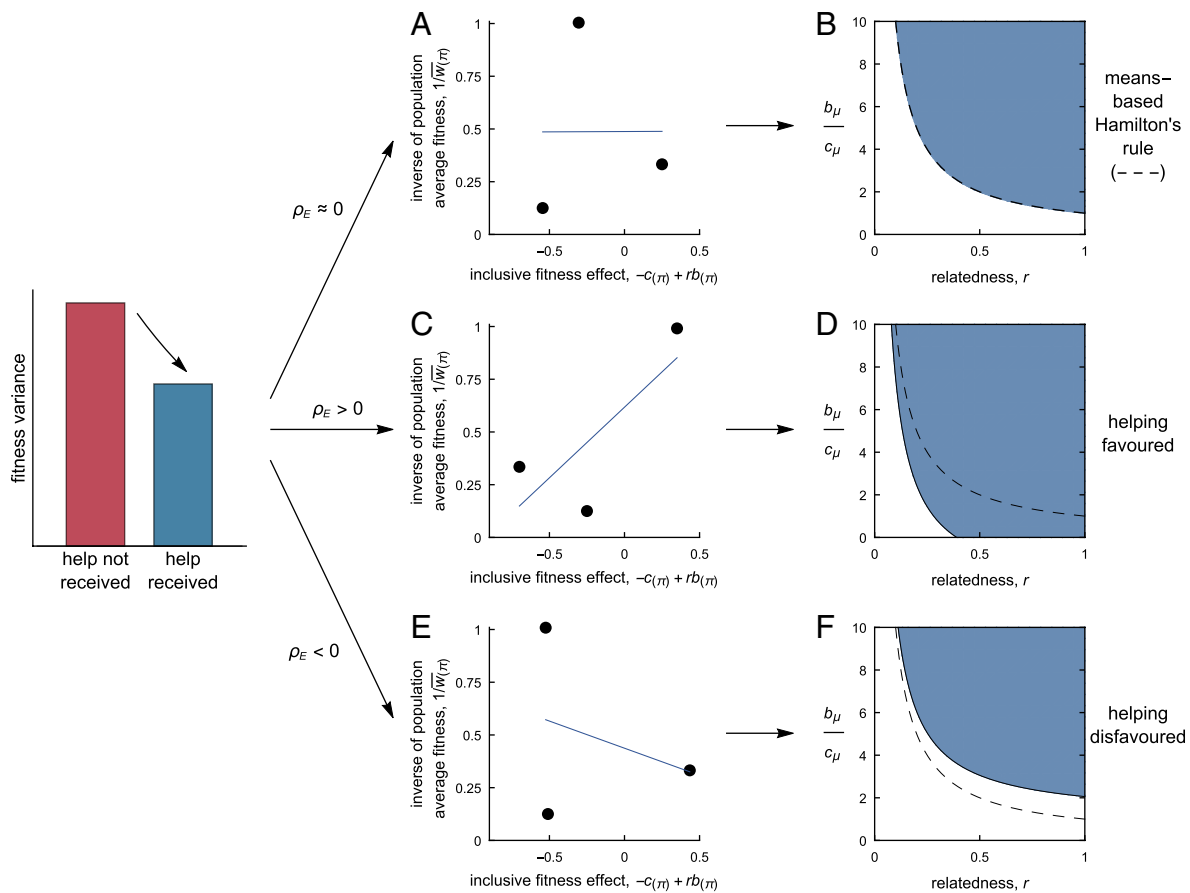


Fig. 2. Natural selection does not consistently favor altruistic bet-hedging. A helping trait that decreases the recipient's reproductive variance can lead to negligible volatility having no effect on altruism relative to the means-based Hamilton's rule (A and B), positive volatility favoring altruism (C and D), or negative volatility disfavoring altruism (E and F). Panels A, C, and E show the correlation between a helping trait's inclusive fitness effects ($-c_{(\pi)} + Rb_{(\pi)}$) and the inverse of population average fitness ($1/\bar{w}_{(\pi)}$) across three equally likely environmental states. B, D, and F show the area of parameter space where helping is favored or disfavored, as a function of relatedness R (x -axis) and the ratio of average benefits b_{μ}/c_{μ} (y -axis). The same patterns would hold with a helping behavior that increases the variance in fitness of relatives (altruistic volatility). In panels B, D, and F, an average benefit b_{μ} is added to each environment-specific benefit $b_{(\pi)}$. Parameters: panels B, D, and F, $c_{(1)} = c_{(2)} = c_{(3)} = c_{\mu} = 0.2$, $\rho = 0.01$, $a_{(1)} = 8$, $a_{(2)} = 3$, $a_{(3)} = 1$. A, C, and E, $R = 0.5$. A and B, $b_{(1)} = -0.69$, $b_{(2)} = 0.9$, $b_{(3)} = -0.21$. C and D, $b_{(1)} = -0.1$, $b_{(2)} = -1$, $b_{(3)} = 1.1$. E and F, $b_{(1)} = -0.62$, $b_{(2)} = 1.27$, $b_{(3)} = -0.65$.

Box 1.

How can natural selection favor costly helping when it *increases* the variance in the absolute reproductive success of relatives? We illustrate this with a simple example, where helping affects the recipient's reproductive variance but not its mean absolute reproductive success (the average benefit is zero). Consider an altruistic helping behavior that increases the recipient's variance in absolute reproductive success across two equally likely environmental states (good and bad environments). We assume that interactions are pairwise in an infinite population of haploid individuals, and that $r = 0.5$. For all individuals, baseline absolute reproductive success in the good and bad environmental state is $a_{good} = 4$ and $a_{bad} = 1$, respectively. The cost of helping is the same across environments, with $c_{good} = c_{bad} = 0.25$. So, helping does not affect the helper's reproductive variance. The "benefit" in good and bad environments is $b_{good} = -3.5$ and $b_{bad} = 3.5$, respectively (to give an average benefit of zero). Hence, receiving help changes the absolute reproductive success of a helper from 3.75 to 0.25, and from 0.75 to 4.25 in the good and bad environment, respectively. When selfish individuals receive help, their absolute reproductive success is changed from 4 to 0.5, and from 1 to 4.5 in the good and bad environment, respectively. So, helping increases any recipient's variance across environmental states from 2.25 to 4. When helping is rare ($\bar{p} = 0.01$), it is favored and increases in frequency ($-c_{\mu} + rb_{\mu} + \nu\rho_E\sigma_{IF} = -0.25 + 0 + 1.03 = 0.78 > 0$). In this case, natural selection favors a helping behavior that increases reproductive variance. To understand the consequences for natural selection, it is necessary to look at how helping influences relative fitness in the different environments. Fitness is by definition relative, measured relative to the population mean (30, 44, 45). In our example, the population mean absolute reproductive success is 3.96 and 1.03 in the good and bad environment, respectively. So, helping decreases the recipient's relative fitness by 0.88 in good environments and increases it by 3.39 in bad environments. Consequently, the benefit in a bad environment outweighs the negative effect in a good environment, giving a positive average effect on recipients across environments ($\mathbb{E}_{\pi}[b_{(x)}/\bar{w}_{(x)}] \approx 1.25$), which favors helping.

Finally, increasing the variance in reproductive success of relatives, at personal cost ("altruistic volatility") can also be favored in some cases (when $\rho_E > 0$; *SI Appendix, Figs. S3–S5*). We illustrate this possibility with a simple numerical example in Box 1. This result is in line with previous theory on nonsocial traits in stochastic environments, which suggested that natural selection can sometimes favor traits with a higher variance (29, 30). It is also consistent with a recent theoretical model of pair-wise cooperation in well-mixed populations that showed how a greater variance in offspring number for cooperators could sometimes revert the direction of selection and favor cooperation (43). We discuss how our results relate to previous theory in more detail in *SI Appendix, Appendix A*.

To summarize, no consistent pattern can be predicted in terms of whether increasing or decreasing the variance in absolute fitness

favors or disfavors altruism. Hence, if an empirical study finds that helping reduces reproductive variance, this does not necessarily imply that this variance reduction favored the helping behavior (32). What matters is how a behavior's net effects vary with the reciprocal mean population absolute reproductive success across environments (whether $\rho_E > 0$), and whether volatility effects are sufficiently large to outweigh the social traits' average effects ($\nu\rho_E\sigma_{IF} > -c_{\mu} + rb_{\mu}$; Fig. 2 and *SI Appendix, Figs. S1 and S2*). Helping is selected for whenever the arithmetic mean relative inclusive fitness effect across environmental states is positive (*SI Appendix, Appendix F*).

Exploring Environmental Variation. We then investigated how often helping can be favored, but where it also leads to an increase in the variance in absolute fitness. We explored a large range of randomly chosen baseline fitness, costs, and benefits in a simple model of pairwise interactions between siblings, with an altruistic and a selfish genotype ($r = 0.5$; *SI Appendix, Fig. S6*). In all parameter combinations, we determined whether helping was favored and whether it either increases or decreases the variance in absolute fitness of relatives. We classified helping as "increasing variance" if both altruistic and selfish individuals had their variance in absolute fitness increased when paired with a helper (other cases were conservatively classified as "decreasing variance"). We found that helping was favored in 17.98% of all cases where it leads to an increase in fitness variation (*SI Appendix, Fig. S6*). In addition, among all cases when helping was favored, it increases variance in 55.6% of cases (*SI Appendix, Fig. S6*). These results suggest that we might often expect to observe helping behaviors that increase fitness variation, if there is large environmental variation ($\nu > 0.5$) and many environmental states.

We also assessed the extent to which using an approximated version of Hamilton's rule leads to errors. In *SI Appendix, Appendix B2*, we demonstrate the mathematical link between our Hamilton's rule and a previous approximated version (18). We find that these two versions of Hamilton's rule agree in the special case when there are only two environmental states that are equally likely to occur (e.g., good and bad years). However, when the two environmental states are not equally likely to occur, or when there are more than two environmental states, these two versions of Hamilton's rule can predict selection in opposite directions. To estimate the approximation's rate of qualitative errors more generally, we performed large sweeps of random parameter values, for 2, 5, 10, and 100 environmental states in our simple model of pairwise interactions (*SI Appendix, Appendix B3 and Fig. S7*). Overall, the approximation predicted selection in the wrong direction in 5.49% of the cases we examined, with this error rate increasing with the coefficient of variation ν , as previously suggested (*SI Appendix, Fig. S7*) (18). Technically, the approximation sometimes correctly predicts that helping can be favored even when it increases variance. However, the approximation sometimes makes such large errors that it is worse at predicting the direction of selection than the simpler means-based version Hamilton's rule ($-c_{\mu} + rb_{\mu}$; *SI Appendix, Fig. S3 E–G*).

Fitness, Geometric Mean Fitness, and Dynamic Sufficiency.

Our results do not contradict the well-known geometric mean fitness principle, which states that successful genotypes in the long term are those which have a higher geometric mean fitness (46). Whether or not the geometric mean is an accurate heuristic to determine the success of an allele depends on the type of stochasticity (within- or between-generation), as well as specific aspects of an organism's life cycle [e.g., whether the population is deme-structured, and if regulation is either global or local in each

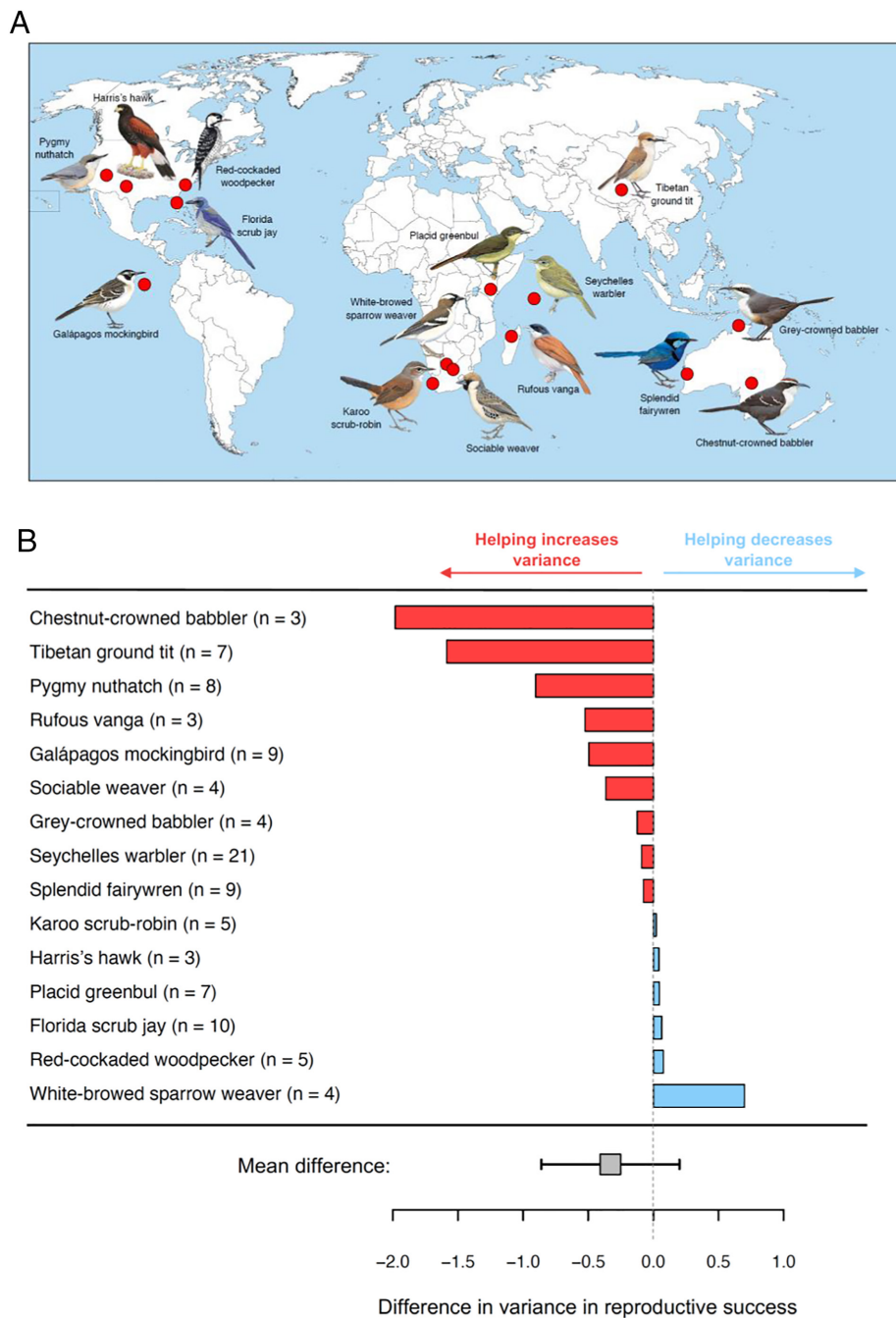


Fig. 3. Variance in reproductive success across cooperatively birds. (A) The global distribution of study species. We collected published data on how helpers affect reproductive success of breeders from 15 bird species. (B) The effect of helping on the variance in reproductive success for each species. Bars show the mean difference in variance in reproductive success between breeding pairs with and without a helper at the nest. Helping does not consistently lead to a decrease in the variance of reproductive success [mean difference = -0.33 , 95% CI = -0.86 to 0.20 , $n = 15$]. The number of breeding seasons sampled is shown in brackets for each species.

deme; (20, 25, 30, 31, 40, 46)]. Our result that higher variance can sometimes be favored is nonetheless consistent with geometric mean arguments, as a genotype can have a higher geometric mean absolute fitness even if it has a higher variance (e.g., if the fitness distribution is skewed; *SI Appendix, Appendix A1 and Table S1*).

Furthermore, our Hamilton's rule stems from the stochastic version of the Price equation (18, 25, 29–31, 40). It can therefore be used as a general framework with few assumptions for decomposing the effect of natural selection, over a single generation, into effects on actors and recipients. Although our approach captures different classes of models, a limitation is that it cannot be used

recursively, to predict the long-term fate of an allele (evolutionary stable strategy). It is therefore dynamically insufficient, in contrast to a few theoretical studies which derived a Hamilton's rule for predicting longer-term evolutionary outcomes in specific models (20, 47). However, in our simulations, we identified simple scenarios where increasing the recipient's variance could be favored over the long term, and the observed steady equilibria were correctly predicted by our Hamilton's rule (*SI Appendix, Fig. S5*). Kennedy et al. also showed that the approximated Hamilton's rule could correctly predict long-term equilibria even with strong autocorrelation between environmental states (18).

Table 1. Volatility parameters and mean fitness benefits in cooperatively breeding birds

Species/population	<i>n</i>	<i>v</i>	ρ_E^b	σ_b	$v\rho_E^b\sigma_b$	b_μ
White-browed sparrow weaver	4	0.51	0.39	0.63	0.13	0.86
Karoo scrub robin	5	0.36	0.58	0.52	0.11	0.69
Tibetan ground tit (pop 2)	3	0.14	0.43	1.05	0.06	1.41
Rufous vanga	3	0.73	0.03	1.02	0.02	1.24
Florida scrub jay	10	0.42	0.17	0.33	0.02	0.88
Placid greenbul	7	0.22	0.58	0.18	0.02	0.06
Red-cockaded woodpecker	5	0.11	0.75	0.24	0.02	0.67
Harris's hawk	3	0.13	0.11	0.32	0.00	0.02
Tibetan ground tit (pop 1)	4	0.09	-0.16	1.09	-0.02	-0.35
Splendid fairy-wren	9	0.19	-0.16	0.67	-0.02	0.77
Pygmy nuthatch (pop 1)	4	0.03	-0.97	1.39	-0.04	0.77
Seychelles warbler	21	0.44	-0.32	0.27	-0.04	0.44
Grey-crowned babbler	3	0.09	-0.91	0.72	-0.06	0.59
Pygmy Nuthatch (pop 2)	4	0.13	-0.59	1.60	-0.12	0.71
Galapagos mockingbird	9	0.80	-0.70	0.53	-0.30	0.26
Sociable weaver	4	0.96	-0.53	0.67	-0.34	0.41
Chestnut-crowned babbler	3	0.43	-0.85	1.54	-0.56	0.66

Each year is considered a different environmental state, and the parameters are calculated using data on the reproductive success of pairs and groups for each population from each year. *n*: number of years/breeding seasons in which reproductive success was measured. *v*: coefficient of variation, ρ_E^b : correlation between helping benefits and the inverse of population average absolute reproductive success. σ_b : SD in helping benefits across years, b_μ : average helping benefit across years.

Empirical Results. We then tested whether helping consistently decreases the variation in reproductive success in cooperatively breeding birds. Reproductive success is a component of fitness that has been commonly estimated in natural populations. We examined data from 17 populations of 15 bird species distributed across the globe (Fig. 3A and *SI Appendix, Appendix E*). We focused on cooperative breeders that raise young in family groups, and where helpers are typically the offspring of at least one of the breeders so that helping can potentially provide indirect (kin-selected) fitness benefits. We compared the reproductive success of individuals receiving help (groups) with those that did not (pairs). For two species (the pygmy nuthatch and the Tibetan ground tit), we had data from two populations which we pooled in our statistical analyses to correctly account for phylogeny.

Fitness Variation in Cooperatively Breeding Birds. We found that helping did not consistently decrease the variance in the reproductive success of breeders (recipients). On average, helping led to an increase rather than a decrease in the variance of reproductive success, although this difference was not statistically significant [mean variance difference across species = -0.33, 95% credible interval (CI) = -0.86 to 0.20; Fig. 3B and see *SI Appendix, Fig. S8*, for the reproductive success data from which the variance for each species was calculated]. We used data on rainfall and temperature variation during the breeding season at each study site to confirm that the lack of an effect of helping on variance in reproductive success is not because studies were carried out in years with relatively little environmental variation (*SI Appendix, Appendix E3 and Fig. S9 D and E*).

A well-known statistical rule in biology is that the variance tends to increase with the mean (Taylor's law). In cooperative breeding birds, groups with helpers have higher mean reproductive success than pairs without helpers (48). We investigated whether our results merely reflected Taylor's law by using the log-transformed ratio of two coefficients of variation ($\ln CVR$) statistical effect size, the logarithm of the ratio of two coefficients of variation (SD/mean). This

allowed us to compare the variance in reproductive success of pairs and groups while accounting for mean differences. When doing this we found very similar results, with helping not leading to a significant decrease in variance in reproductive success ($\ln CVR = 0.37$, CI = -0.28 to 0.77; *SI Appendix, Fig. S9F*). When scaling for the mean, helping decreased variance in reproductive success in six species (6/15 = 40%), and increased it in the other nine species (60%).

We suggest two hypotheses for the lack of a consistent effect of helping on variance in reproductive success. First, the impact of helping on fitness variance may have a negligible influence on selection for helping, relative to the influence of mean fitness. Formally, this would represent the volatility effect in inequality 1 being negligible compared to classic means-based components of Hamilton's rule. The second possibility is that the influence of helping on the variance of fitness does influence selection, but it does so in different directions in different species. This possibility also follows from inequality 1, which shows that natural selection can favor behaviors that either increase or decrease the recipients' fitness variance. In the next section, we use the data from cooperatively breeding birds to test between these two competing hypotheses.

Parameterizing Volatility Effects in Cooperatively Breeding Birds. We then used the reproductive success data from these cooperatively breeding bird species to estimate the benefit parameters in our Hamilton's rule (Inequality 1). We had to focus on how helping influences the benefit of helping for the same reason as previous studies (18, 32). The reason for this is that an examination of the costs of helping requires data on parameters that are hard to estimate. In particular, the likelihood that helpers could have been able to independently breed varies from 0 to 100%. Perhaps helpers could have successfully bred, or perhaps there were insufficient quality territories, or they were too low quality to breed without helpers. This means that the cost of helping could be anything from 0 to the mean reproductive success of pairs that breed without helpers.

The available data allowed us to examine the benefits of helping, and how this varies across different environmental states (years)

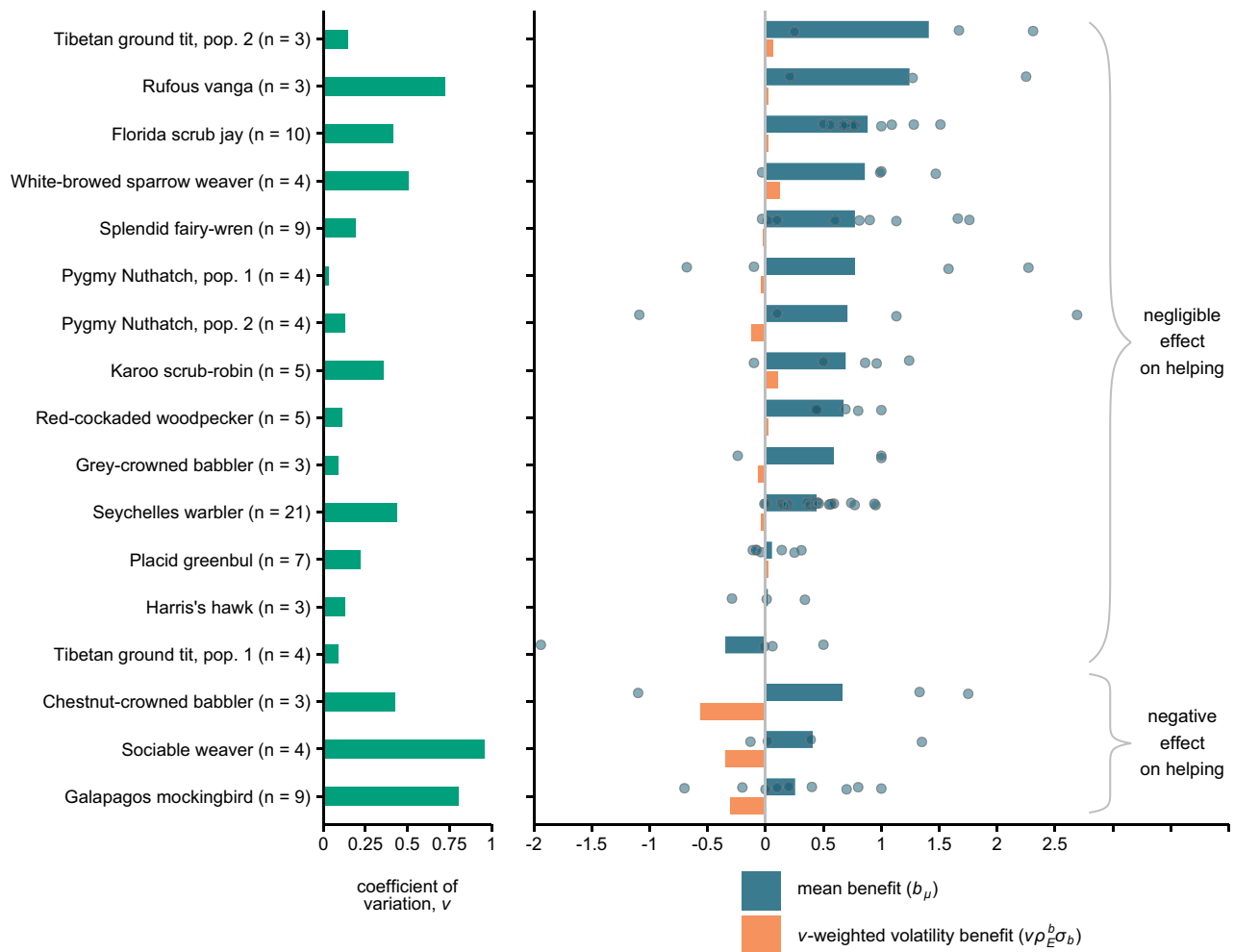


Fig. 4. Volatility versus mean fitness benefits in cooperatively breeding birds. Coefficient of variation (ν ; green bars), mean benefits of helping (b_μ ; blue bars), and the ν -weighted volatility benefit ($\nu\rho_E^b\sigma_b$; orange bars) for each population. The sample size n for each species is shown in brackets (number of years). In 14 populations, the ν -weighted volatility benefit is negligible compared to the mean benefit. In three populations, volatility is appreciable and disfavors rather than favors cooperation. The number of breeding seasons sampled is shown in brackets for each species.

for each of the 17 populations (Table 1 and *SI Appendix, Appendix E2*). In *SI Appendix, Appendix B1*, we show how to decompose the volatility effect from Inequality (1) into its separate volatility cost ($\rho_E^c\sigma_C$) and volatility benefit ($\rho_E^b\sigma_b$), both weighted by the coefficient of variation ν . This decomposition allows us to focus on parameterizing the effects from receiving help in inequality (1) with the existing data ($\rho_E^b\sigma_b$). In turn, we can then examine whether variation in the benefit of helping has had an influence on the evolution of altruistic helping.

We found that the mean benefit of helping was significantly greater than the volatility benefit across populations, suggesting little effect of environmental variation on selection for helping (Fig. 4 and Table 1; mean benefit $b_\mu = 0.58$, CI = 0.20 to 0.83; ν -weighted volatility benefit $\nu\rho_E^b\sigma_b = -0.04$, CI = -0.21 to 0.10; $N_{\text{populations}} = 17$, $N_{\text{species}} = 15$, difference $P < 0.01$; *SI Appendix, Fig. S9A*). In 14 out of 17 populations, the ν -weighted volatility benefit was negligible compared to the mean benefit. Specifically, in these 14 populations the ν -weighted volatility benefit was between 2.5 and 52.6 orders of magnitude smaller than the mean benefit (~ 16 times on average), suggesting no or very little effect of the ν -weighted volatility benefits of helping on selection (Fig. 4). The three populations where the ν -weighted volatility benefits were non-negligible are the Galapagos mockingbird, the sociable weaver, and the chestnut-crowned babbler (37, 49, 50). The mainly

positive mean benefits from helping we found suggest that the data are reliable. Furthermore, in 9 out of 17 populations, including the only three where volatility benefits were appreciable, the benefit part of fitness–environment correlation coefficient was negative ($\rho_E^b < 0$), meaning that environmental variation disfavors rather than favors helping (Fig. 4 and Table 1). Therefore, even though our theory predicts that natural selection can sometimes favor helping that increases variance, we did not find such cases in species when volatility effects were non-negligible.

If we had instead used the approximated version of Hamilton's rule (18), then we would have largely overestimated the beneficial effect of helping (between 1.9 and 3.6 orders of magnitude) in three species (the chestnut crowned babbler, the Galapagos mockingbird, and the sociable weaver; *SI Appendix, Fig. S10*). In addition, in the Galapagos mockingbird, the approximation would have led to the incorrect conclusion that helping was beneficial, when in fact reduced the reproductive success of those being "helped."

Conclusion

Our Hamilton's rule predicts that natural selection does not consistently favor helping behaviors that reduce the fitness variance of related breeders. Natural selection can sometimes disfavor helping that decreases variation in absolute fitness, even in cases

when helping is personally beneficial to the actor. Selection can also sometimes favor costly helping that increases variation in absolute fitness. Hence, determining whether a trait is favored due to its influence on variation in absolute reproductive success requires either parameterizing the volatility part in Inequality 1, or estimating the trait's effects on relative fitness directly (40, 44, 51, 52). Our empirical results from cooperative birds suggest that 1) helping does not consistently reduce the variance in the reproductive success of related breeders; 2) the effect of helping on the recipients' volatility is mostly negligible compared to the effect of helping on mean fitness (classical means-based Hamilton's rule). However, our empirical analysis should be seen as a preliminary step, as we examined a fraction of all the cooperatively breeding bird species. Further diversity from a range of taxa would also be very useful. Also, we have focused on how environmental variability influences the benefit of helping. We cannot exclude the possibility that the mean and volatility costs make up a large part of Hamilton's rule in the species we analyzed. Key steps for future empirical studies are therefore to collect data on how the cost of helping and relatedness vary across environmental conditions and to examine the consequences of helping on relative fitness directly (44, 45, 52).

Materials and Methods

Derivation. We derive Hamilton's rule for a variable environment. Our starting point is the prospective Price equation (18, 25, 29–31, 40), which focuses on the expected change in population average genetic value across all possible environmental states that a population may experience. This expected change in average genetic value across states is given by the expected covariance across environmental states between individual genetic value and relative fitness. We then apply Queller's method to express absolute fitness in each environmental state as a multiple linear regression (10). With additional rearrangements,

we are able to separate mean effects from all the other effects (means-based Hamilton's rule and volatility effects, respectively), and express the volatility effects in a way that is easily interpretable for empirical researchers (a coefficient of variation, a correlation, and a SD). The full derivation is presented in *SI Appendix, Appendix A*.

Data on Cooperatively Breeding Birds. We collected published data on the reproductive success of pairs and groups of cooperative breeding birds across several breeding seasons to estimate both the average and volatility benefit from our version of Hamilton's rule in a variable environment. Data were obtained from 15 studies, which represent 17 populations from 15 bird species (either publicly available or obtained from the authors directly). To quantify how variable sampled years were for each population in our dataset, we extracted data on the mean breeding season rainfall and temperature from 1901 to the end of each study for each study location from the Climatic Research Unit Time-Series. The full details of the data collection are presented in *SI Appendix, Appendix E*.

Data, Materials, and Software Availability. Simulation data, generated using:—R: A language and environment for statistical computing, v.4.3.0—Julia v. 1.9.4 data have been deposited in Open Science Framework (<https://osf.io/8mc3n/>) (53). Previously published data were used for this work. Data from published studies on the reproductive success of pairs and groups of cooperative breeding birds across several breeding seasons were compiled. These data were obtained from 15 studies, representing 17 populations from 15 bird species, either publicly available or obtained directly from the authors. All citations are provided in the *SI Appendix*.

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