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No evidence for a heritable altruism polymorphism in Tibetan ground tits

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A recent study in PNAS on Tibetan ground tits (1) concludes that inclusive fitness maintains heritable altruism polymorphism if $rb = c$, which may render equal inclusive fitness in helpful and unhelpful genotypes. We outline flaws in the estimations of $rb = c$ and additive genetic variance, and we propound that current evidence is lacking to justify the conclusions. Sufficient evidence requires that (*i*) helping yields similar benefits to nonhelping, while adequately controlling for potential confounds; and (*ii*) altruism is heritable.

First, support for $rb = c$ depends on the validity of the inclusive fitness estimate, which is flawed in the paper by Wang and Lu (1) for the following reasons:

i) Hamilton's rule asserts that altruistic traits can spread within populations if the product of the degree of relatedness, r, and the recipient's benefit, b, is greater than the actor's costs, c (2). The calculation of b in ref. 1 was based on the reproductive success of helped individuals relative to all others, rather than only nonhelped ones. Hence, b is underestimated, suggesting that, in fact, $rb > c$.

ii) Interindividual variation in the amount and types of help was not accounted for in the calculations of inclusive fitness (1), further obscuring the estimation of b and c.

iii) It is unclear whether ever- and never-helping individuals received help as breeders (figure 3B of ref. 1). Helpers' indirect fitness benefits were not deducted from breeders' direct fitness benefits (1), which are therefore overestimated by double accounting. The inclusive fitness of breeders never giving help was unjustifiedly overestimated and may actually be lower than (and not equal to) that of individuals who helped (thus, $rb > c$).

iv) Calculations of b and c in ref. 1 did not fully account for territory quality effects on offspring production and helper presence (3, 4). The most parsimonious explanation of the results may be territory quality variation instead of behavioral differences. Territory quality was estimated by the number of fledglings produced in a territory, reflecting an obvious circular argument, since the number of offspring produced was also the dependent variable. If high-quality territories are more likely to produce offspring and to have helpers, the additional offspring may be attributed to territory quality rather than to apparent indirect fitness (4).

Second, random effects in animal models often include additive genetic, maternal, and environmental effects (5, 6), instead of an uninformative prior (1). Repeated records per individual appear available (1) to test for variance dependencies on age (5). There are likely genetic and nongenetic sources of phenotypic similarity (5) other than the covariance of shared genes as determined from the pedigree and sex (1). These omissions have likely inflated the heritability estimate of helping (5, 6).

Evidence of variation in helping (1) is insufficient to support altruism polymorphism genotypes without considering causation and environmental effects on potential conditional alternative life history phenotypes (7). While it is worth pursuing to ask whether $rb = c$ can predict the persistence of a stable heritable altruism polymorphism, we stress that if helping is a conditional strategy, then polymorphism can be maintained under any relation between rb and c.

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