

# Kin Discrimination and the Benefit of Helping in Cooperatively Breeding Vertebrates

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In many cooperatively breeding vertebrates, a dominant breeding pair is assisted in offspring care by nonbreeding helpers. A leading explanation for this altruistic behavior is Hamilton's idea that helpers gain indirect fitness benefits by rearing relatives (kin selection). Many studies have shown that helpers typically provide care for relatives, but relatively few have shown that helpers provide closer kin with preferential care (kin discrimination), fueling the suggestion that kin selection only poorly accounts for the evolution of cooperative breeding in vertebrates. We used meta-analysis to show that (i) individuals consistently discriminate between kin, and (ii) stronger discrimination occurs in species where the benefits of helping are greater. These results suggest a general role for kin selection and that the relative importance of kin selection varies across species, as predicted by Hamilton's rule.

In cooperatively breeding vertebrates, a dominant pair usually produces the majority of the offspring, whereas the cost of caring for offspring is shared by nonbreeding subordinates (1–5). Explaining how this and other altruistic helping behavior by nonbreeders is maintained by natural selection is a major problem for evolutionary biology. Hamilton's hugely influential kin selection theory provides a possible solution to this problem by pointing out that subordinates can gain indirect fitness benefits by helping relatives (6, 7). However, although kin selection appears to play a crucial role in understanding social insects (8, 9), its potential importance in vertebrates has been much debated (1–4, 9, 10). Groups in cooperatively breeding species are typically made up of extended families, suggesting that subordinates will often be helping relatives (11). However, these associations between relatives can result from limited dispersal of individuals, and the relatedness among group members is not necessarily lower in species that live in stable groups but do not breed cooperatively (1, 10). Furthermore, it is increasingly realized that there are a number of ways in which subordinates may gain direct fitness benefits by helping to raise offspring, such as the survival benefits of increasing group size (1, 2, 10, 12–14).

The most fundamental way to test for a role of kin selection is to test whether the probability or amount of helping covaries with genetic relatedness between potential helpers and beneficiaries. Relatedness between group members varies within groups because of immigration and changes in the

identity of the breeding dominants. Helpers can potentially assess their relatedness to other group members through a variety of direct or indirect mechanisms (15, 16). Kin selection theory predicts that there will be a positive correlation between the probability or amount of help and relatedness, with helpers preferentially aiding closer relatives (kin discrimination). Although many long-term studies on vertebrates have addressed this problem, there is no clear pattern, with some finding that individuals provide greater levels of help to closer relatives (17–19) and others not (20–23). Consequently, although some authors have argued that the overall pattern provides strong support for a role of kin selection, others have argued that there is insufficient consensus to support a generally important role of kin selection (1, 2, 4, 9). This debate can only be resolved by explaining the variation that exists across species in the degree of kin discrimination.

Our aims here are to determine whether (i) kin selection is of general importance in vertebrates and (ii) variation in the level of kin discrimination across species can be explained by kin selection theory. A useful

methodology for such quantitative comparison across species is meta-analysis (24, 25), which takes a standard measure of the magnitude of the statistical effect from each study (hereafter called effect size) and uses it as the response variable in a comparative analysis. The effect size used is  $r$ , the correlation coefficient, which varies between  $\pm 1$ . In the case examined here, we utilize the correlation coefficient of the relationship between probability or amount of help given and relatedness, which we define as  $r_{\text{kin}}$ . Larger positive values of  $r_{\text{kin}}$  represent a more precise positive correlation between the levels of helping and relatedness, with the value of  $r^2_{\text{kin}}$  representing the proportion of variance in the level of helping that can be explained by variation in relatedness. We were able to collect relevant data testing the relationship between level of helping and relatedness from studies on 18 cooperatively breeding vertebrate species: 15 birds and 3 mammals [table S1 (26)]. We carried out all analyses with standard meta-analytic methods (27).

Overall, these studies show a significant pattern of kin discrimination, with helpers preferentially aiding closer relatives. The estimated mean effect size of kinship on helping behavior was  $r_{\text{kin}} = 0.33$  and was significantly larger than zero [ $P < 0.01$  (Table 1 and Fig. 1)]. This is a relatively strong effect when compared with the average effect size of  $r \approx 0.19$  for ecological and evolutionary variables (28) and suggests that, on average, approximately 10% of the variation in helping rates can be explained by relatedness. The significant mean effect size holds when analyzing mammals and birds separately, when studies on all forms of altruistic behavior are included, and when allowing for publication bias (24, 25, 29) [Table 1 and table S1 (26)]. Furthermore, the mean effect size suggests one reason why some studies show significant effects and others do not: With a mean  $r_{\text{kin}} = 0.33$ , the sample size required to reject the null hypothesis with 80% certainty at  $P = 0.05$  is 76, which can be difficult to obtain in studies of cooperative breeding vertebrates, especially when replicating at the group level (24, 25, 29) [table S1 (26)].

**Table 1.** Summary of standardized effect sizes for studies of kin discrimination in vertebrates.

Class of study	Mean $r_{\text{kin}}$	95% CI <sup>‡</sup>	Species (n)
Offspring care	0.314 <sup>†</sup>	0.129–0.493	18
Birds	0.337 <sup>†</sup>	0.106–0.550	15
Mammals	0.238 <sup>†</sup>	0.185–0.283	3
Probability of help	0.470 <sup>†</sup>	0.269–0.661	9
Amount of help	0.180	–0.016–0.409	10
Sample size (n) = number of groups	0.364 <sup>†</sup>	0.143–0.565	15 <sup>§</sup>
All cooperative behavior*	0.307 <sup>†</sup>	0.138–0.522	22

\*Includes behaviors other than offspring care, such as guarding and foraging (26). †Significantly greater than zero, with  $P < 0.01$ . ‡Obtained by bootstrapping. §Studies were omitted when the number of groups could not be ascertained or was  $\leq 3$  (26).

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The extent of kin discrimination varies widely across species, with the effect size  $r_{kin}$  ranging from  $-0.29$  to  $0.88$ . To what extent can this variation be explained by kin selection theory? In order to address this question, it is useful to consider the quantification of kin selection theory provided by Hamilton's rule (7): Cooperative behavior will be favoured if  $Rb - c > 0$ , where  $R$  is the genetic relatedness between the helper and the offspring helped,  $b$  is the fitness benefit to the offspring helped, and  $c$  is the fitness cost of helping (6). Hamilton's rule predicts that the level of kin discrimination would also be

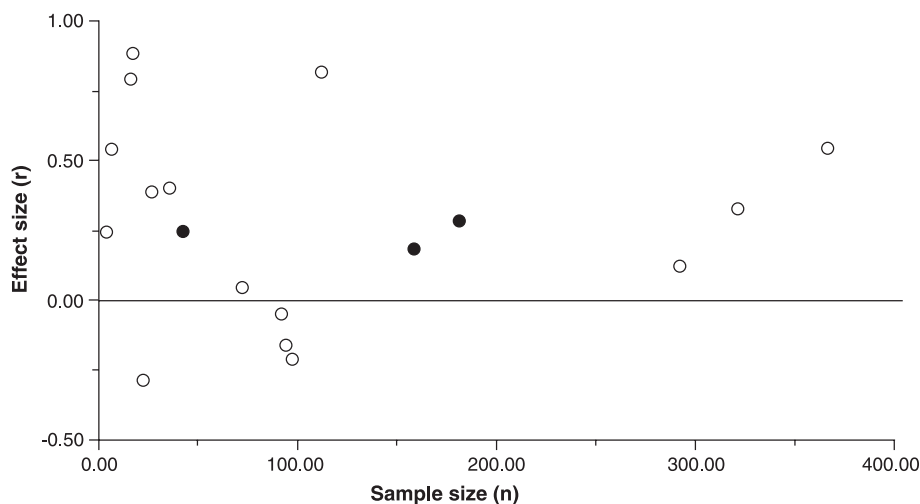
expected to vary with the cost ( $c$ ) or benefit ( $b$ ) of helping. Kin discrimination will therefore be most favored when the costs of helping are low and the benefits high.

Considering the cost ( $c$ ) of helping, Emlen and Wrege (19) suggested that kin discrimination would be more likely to be seen in studies measuring the probability of help than in those measuring the amount of help given. They argued this on the grounds that the amount of help given may be more likely to also depend on other factors, such as the helper's physical condition, which can influence the cost of helping. We tested this hypothesis and found that al-

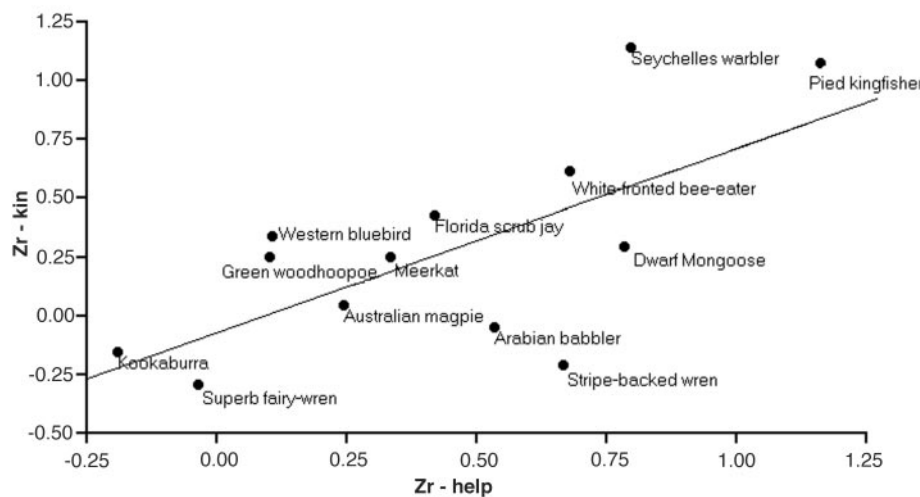
though the data are in the predicted direction, with the mean effect size  $r_{kin} = 0.47$  and  $0.18$  for probability and amount of help respectively (Table 1), this difference is nonsignificant ( $Q = 4.14$ ; randomization test gives  $P = 0.09$ ). This nonsignificant result could be explained if individuals also make condition-dependent decisions on whether to become a helper. Nonetheless, it would be extremely useful to collect more empirical data addressing this possibility, especially paired within-species comparisons.

Another possible explanation for variation in the extent of kin discrimination is that the benefit ( $b$ ) of helping varies across species. Hamilton's rule (6) predicts that altruism is more likely to be favored as the benefit to the helped individual increases (6). We can estimate the benefits of helping to raise offspring by measuring the effect size of the relationship between offspring production/survival and the amount of help given, hereafter defined as  $r_{help}$ . Consequently, we can test the prediction that kin discrimination and the preferential helping of relatives will be more likely in species where the benefits of helping are greater, by examining whether  $r_{kin}$  is positively correlated with  $r_{help}$ . We were able to find data on the benefits of helping ( $r_{help}$ ) in 13 of the species where we have data on the extent to which related offspring are preferentially helped ( $r_{kin}$ ) [table S2 (26)]. In these species, helping provided a consistently positive benefit to the individuals helped (mean  $r_{help} = 0.41$ , 95% confidence interval (CI) =  $0.21$  to  $0.61$ ,  $n = 13$  species, significantly greater than zero  $P < 0.01$ ).

Across species, as predicted by Hamilton's rule, we found that kin discrimination was more likely in species where helping provides greater benefits (higher  $b$ ):  $r_{kin}$  was positively correlated with  $r_{help}$  [slope =  $0.78$ , SE =  $0.30$ , randomization test ( $P_{rand}$ ) =  $0.01$ ,  $n = 13$  species (Fig. 2)]. This result provides an adaptive explanation for some of the variation across studies in the occurrence of kin discrimination. Specifically, it suggests that some species in which nonsignificant results were obtained represent cases where there are relatively small benefits to helping (low  $b$ ), and so kin selection for helping will be weak or nonexistent. In these cases, helping may be maintained primarily by direct fitness benefits (1, 2, 10, 13, 14). Overall, our result explains 42% of the variation across species in the extent of kin discrimination. Furthermore, our result provides a lower limit on the ability of kin selection to explain variation in  $r_{kin}$ , because there may also be variation in the ease and importance of kin discrimination for other reasons that have not been sufficiently quantified to test. For example, if cooperative groups consist of only or predominantly close relatives, then even indiscriminate helping would be favored by kin selection, leading to possibilities of high  $r_{help}$  and low  $r_{kin}$ , as occur in the stripe-backed wren (30).



**Fig. 1.** Kin discrimination in vertebrates. The effect size of the relationship between level of help and relatedness ( $r_{kin}$ ) is plotted against the sample size of the study. A positive value of  $r_{kin}$  corresponds to helpers preferentially helping closer relatives, whereas a negative value corresponds to the opposite pattern. The significant trend toward positive values ( $P < 0.01$ ) indicates that vertebrates consistently provide greater levels of help to closer relatives, as predicted by kin selection theory. The different symbols represent birds (open circles) and mammals (solid circles).



**Fig. 2.** Correlation between kin discrimination and the benefits of helping. The effect size of the relationship between level of help and relatedness ( $Z_r$  transformation of  $r_{kin}$ ) is plotted against the effect size of the relationship between the benefit of helping and the level of helping ( $Z_r$  transformation of  $r_{help}$ ). The significant positive relationship between these two variables ( $P = 0.01$ ) indicates that preferential helping of relatives (kin discrimination) is more likely in species where there are greater fitness benefits from helping, as predicted by kin selection theory.

## REPORTS

Our results provide support for a role of kin selection in favoring helping behavior within cooperative vertebrates. Moreover, we show that the importance of kin selection varies across species, consistent with the predictions of Hamilton's rule (6). Specifically, preferential helping of relatives is more common in species where helping provides a greater benefit. It should be noted that our results do not imply that the direct fitness benefits of helping are unimportant or show anything about the relative importance of direct and indirect fitness benefits. Ideally, the next step would be an equivalent study on the effect size of direct fitness benefits.

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27. We used standard meta-analytic methods, described in detail elsewhere (25), implemented with the package MetaWin 2.0 (31). Effect sizes from each test statistic were averaged to obtain a single value per species. Effect sizes were Z-transformed before analysis to correct for the asymptotic behavior of  $r$ , and in all analyses individual effect sizes were weighted by the inverse of the variance associated with the effect size estimate. We used random effect models, because these are more appropriate for ecological data, and our underlying hypothesis is that effect sizes may differ between species.
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29. Several lines of evidence suggest that the pattern observed was not greatly affected by publication bias: the tendency to publish only significant results (24, 25, 31, 32). First, the subject area is one in which

there can be as much incentive to publish nonsignificant results as significant results. Second, a scatter plot of effect size versus sample size did not show a pattern suggesting missing data for cases with nonsignificant effect sizes and small sample sizes (Fig. 1). Third, the rank correlation coefficient between effect size and sample size was not significantly negative ( $R_s = -0.14$ ,  $P = 0.58$ ). Fourth, we calculated the "fail-safe number," which is the number of unpublished studies with an effect size of zero that would have to exist in order for the overall mean effect size to be not significantly different from zero. The fail-safe number was 71, which suggests that our result is extremely robust, because there are unlikely to be unpublished studies with  $r_{kin} = 0$  on this many species. Fifth, we used the trim and fill method of Duval and Tweedie (33) to estimate the number of missing studies and their effect sizes (32). This method estimated that there were no missing studies ( $L_o = 0$ ). Sixth, a common problem in studies on cooperative breeding vertebrates is pseudoreplication. In many cases where the appropriate independent data point is a group, data has been analyzed using individuals or multiple observations from individuals. However, even when we analyzed the data weighting studies by the number of groups rather than the given sample sizes, the mean effect size was

still significantly greater than zero (Table 1). Seventh, we found no significant difference in the effect size between studies based on pedigree or genetic data ( $P_{rand} = 0.28$ ), suggesting that how relatedness was measured was not biasing the results.

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34. We thank A. Russell, B. Sheldon, D. Shuker, and three anonymous referees for comments; L. Bennun, P. Finn, and A. Russell for supplying and clarifying data; M. Jennions for supplying a spreadsheet for trim and fill analyses; and the Natural Environment Research Council, Biotechnology and Biological Sciences Research Council, and Royal Society for funding.

### Supporting Online Material

www.sciencemag.org/cgi/content/full/302/5645/634/DC1

Materials and Methods

Tables S1 and S2

References

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# BRCT Repeats As Phosphopeptide-Binding Modules Involved in Protein Targeting

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We used a proteomic approach to identify phosphopeptide-binding modules mediating signal transduction events in the DNA damage response pathway. Using a library of partially degenerate phosphopeptides, we identified tandem BRCT (BRCA1 carboxyl-terminal) domains in PTIP (Pax transactivation domain-interacting protein) and in BRCA1 as phosphoserine- or phosphothreonine-specific binding modules that recognize substrates phosphorylated by the kinases ATM (ataxia telangiectasia–mutated) and ATR (ataxia telangiectasia– and RAD3-related) in response to  $\gamma$ -irradiation. PTIP tandem BRCT domains are responsible for phosphorylation-dependent protein localization into 53BP1- and phospho-H2AX ( $\gamma$ -H2AX)–containing nuclear foci, a marker of DNA damage. These findings provide a molecular basis for BRCT domain function in the DNA damage response and may help to explain why the BRCA1 BRCT domain mutation Met<sup>1775</sup> → Arg, which fails to bind phosphopeptides, predisposes women to breast and ovarian cancer.

Signal transduction by protein kinases in eukaryotes results in the directed assembly of multiprotein complexes at specific locations within the cell (1). This process is particularly evident after DNA damage, where activation of DNA damage response kinases results in the formation of protein-protein complexes at discrete foci within the nucleus (2). In many cases, protein kinases directly control the formation of these multiprotein complexes by generating specific phosphorylated-motif se-

quences; modular binding domains then recognize these short phospho-motifs to mediate protein-protein interactions (3, 4).

We used a proteomic screening approach (5) to identify novel modular pSer- or pThr-binding domains involved in the DNA damage response. In cells exposed to  $\gamma$ -irradiation, the kinases ATM and ATR phosphorylate transcription factors, DNA repair proteins, protein kinases, and scaffolds on Ser-Gln and Thr-Gln motifs (6). We therefore constructed an oriented phosphopeptide library biased to resemble the motif generated by ATM and ATR (7, 8) (Fig. 1A). This library and its nonphosphorylated counterpart were immobilized and screened against ~96,000 in vitro translated polypeptides (960 pools each containing ~100 transcripts) (Fig. 1A).

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