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First evidence for heritable variation in cooperative breeding behaviour

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Understanding the evolution of complex social behaviours, such as cooperative breeding, is a fundamental problem in evolutionary biology, which has attracted much theoretical and empirical interest. Variation within and between species in the frequency of helping behaviour has been typically associated with variation in direct costs and benefits due to ecological constraints, or with indirect fitness payoffs (i.e. kin selection). Here, we provide the first evidence that individual variation in cooperative behaviour within a natural population also has a heritable component. Using a seven-generation pedigree in a wild population of western bluebirds (*Sialia mexicana*), we show significant heritable variation for the propensity to help rather than breed, as well as for the probability of having a helper at the nest. We also document a strong positive relationship between a bird's lifespan and its prospect of receiving help when breeding, in accordance with earlier comparative studies across species. These findings provide useful insights into the possible mechanisms which have led to the evolution of cooperative breeding and other social systems.

Keywords: cooperative breeding; heritability; life-history theory; lifespan; *Sialia mexicana*; western bluebirds

1. INTRODUCTION

The origin of complex social behaviours (Maynard Smith & Szathmáry 1995), such as eusociality or cooperative breeding (Andersson 1984), raises a fascinating set of problems in evolutionary biology. Despite a wealth of theoretical and empirical studies on the evolution of social behaviour (Andersson 1984; Stacey & Koenig 1990; Koenig & Dickinson 2004), surprisingly little is known about the genetic basis of these traits within natural populations. However, two recent studies have identified genes that appear to influence social behaviour. Differences in mating behaviour between monogamous prairie voles (*Microtus ochrogaster*) and their promiscuous relative, the meadow vole (*Microtus pennsylvanicus*), are linked to the presence of the vasopressin receptor in the brain (Lim *et al.* 2005), although recent findings highlight a more complex genetic control than initially suggested (Fink *et al.* 2006). Within populations of the fire ant, *Solenopsis invicta*, the distinction between monogyne and polygyne colonies appears to be due to allelic variation at a single gene, *GP-9* (Krieger & Ross 2002). Such findings run contrary to the traditional claim that, at least within populations, variation in social behaviour can be explained by either relatedness or the balance between the costs and benefits of the behaviour and the ways in which those costs and benefits are shaped by extrinsic factors (e.g. Koenig & Dickinson 2004).

Cooperative breeding, where individuals other than the male–female pair help to raise a single brood (Brown 1987), has been recorded in 9% of bird species (Cockburn 2006).

The wide variation observed in the occurrence of helping behaviour has spawned an abundant literature in birds as well as in mammals and insects. Many selective forces may favour individuals that help others before producing their own offspring, including delayed dispersal, environmental constraints such as food shortage, high predation rate and the opportunity to increase inclusive fitness (Brown 1987; Stacey & Koenig 1990; Cockburn 1998). Typically, these factors are invoked to explain differences in helping behaviour between species rather than within species (but see Komdeur 1992, 2003; Covas *et al.* 2004), but even when considered together, they cannot account for the range of variation observed in cooperative behaviour among species (Stacey & Koenig 1990).

Phylogenetic studies suggest a role for genetics in helping behaviour, since related species that are ecologically distinct often show similar cooperative behaviour (Cockburn 1996; but see Nicholls *et al.* 2000; Ekman & Ericson 2006). The so-called ‘phylogenetic inertia’ hypothesis (Edwards & Naem 1993), in which cooperative breeding persists in lineages even when there are no selective forces favouring it, could explain the apparent lack of fitness benefits for helpers that has been found in several species (Sappington 1977; Du Plessis 1991; Dickinson 2004b). Surprisingly, little attention has been paid to whether cooperative breeding behaviour displays any heritable variation or is genetically correlated with other traits (Komdeur 2006).

Here, we investigate whether intrinsic genetic factors explain a significant component of the variation observed in cooperative breeding behaviour within a wild vertebrate population. We use a long-term pedigree of individually marked western bluebirds (*Sialia mexicana*) to estimate the heritability of helping behaviour as well as to examine the relationship between fitness traits and the probability of receiving help when breeding.

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2. MATERIAL AND METHODS

(a) Population and pedigree

From 1995 to 2002, the Prescott Bluebird Recovery Project monitored approximately 2700 breeding attempts by western bluebirds (*S. mexicana*) in 1900 nest boxes distributed in rural, agricultural and suburban areas in Oregon (see electronic supplementary material for details on the population and habitats). These boxes were initially erected in known western bluebird territories and they are now the primary nesting sites for the birds (Keyser *et al.* 2004). Over the winter, family groups defend territories around nest boxes in which they roost, and which most often later become their breeding sites (Kraaijeveld & Dickinson 2001). A supplemental feeding experiment was conducted on 1083 breeding attempts during the nestling period between 1997 and 2002 (Keyser *et al.* submitted; electronic supplementary material). The reconstructed pedigree of breeding birds includes 1593 individuals over seven generations (see electronic supplementary material for more details). Of these 1593 breeders, 29% were supplemented when they were nestlings and 43% were supplemented when they were breeding adults; 97% are of known cohort year, 99% of known sex (20 unsexed birds) and 57% are of known lifespan.

(b) Estimating heritability of helping behaviour

Being a helper (yes/no) and receiving help when breeding during one or more breeding attempts (yes/no) were considered threshold traits. This means that for each trait, the two options are determined by an underlying continuous distribution, or 'liability' (Falconer & Mackay 1996; Lynch & Walsh 1998) with a threshold of sensitivity. Individuals with liabilities above the threshold are helpers (or receive help) whereas those below are not. Based on this assumption, we estimated heritability for both traits using a pedigree-based restricted maximum-likelihood animal model (Knott *et al.* 1995). First, we determined factors that influenced being a helper or receiving help, in order to include them as fixed effects in the animal model. We performed generalized models with a binary error distribution to investigate whether the traits were influenced by food supplementation at the nestling or adult life stage, cohort year, sex and lifespan and all corresponding interactions. After removing non-significant terms ($p > 0.05$) from the initial saturated model, being a helper was found to be influenced only by the sex of the individual (1.3% of females were helpers versus 6.5% of males, $F_{1,897} = 18.54$, $p < 0.0001$). Receiving help when breeding was influenced by nestling food supplementation (9.8% of supplemented individuals received help when breeding versus 5.9% of non-supplemented individuals, $F_{1,912} = 4.79$, $p = 0.029$) and individual lifespan (the longer the lifespan, the higher the chance of being helped, $F_{1,912} = 49.91$, $p < 0.0001$). Although adult food supplementation seemed to increase the likelihood of receiving help (10.7% of supplemented adults versus 6.5% of non-supplemented adults received help when breeding), this factor was not significant in the final model and was removed.

Second, we estimated genetic variance components assuming a Gaussian distribution for liabilities of both traits (being a helper and receiving help) in a multivariate restricted estimate maximum-likelihood procedure implemented in the program ASREML (Gilmour *et al.* 2002). Both traits were analysed simultaneously, using a bivariate animal model (Knott *et al.* 1995; Kruuk 2004) where sex, nestling supplementation and lifespan were included as fixed effects.

Each individual phenotype was broken down into its components of additive genetic value and residual error, while controlling for fixed effects. The total phenotypic variance for each trait could then be described as $V_P = V_A + V_R$, where V_A is the additive genetic effect and V_R is the residual variance. Our sample size did not allow us to include further random effects. The narrow-sense heritability on the dichotomous scale is defined by $h_d^2 = V_A/V_P$ (Falconer & Mackay 1996). Finally, we converted heritability estimates obtained above to a continuous liability scale using the equation $h_c^2 = h_d^2 p(1-p)/z^2$, where p is the incidence in the population and z is the height of the standardized normal distribution for this incidence (Hill & Smith 1977; Falconer & Mackay 1996).

Heritability for both traits was also estimated using a simple threshold model following Edward's equation (Edwards 1969; Lynch & Walsh 1998), which approximates the parent-offspring correlation for liability using population incidences.

(c) Factors influencing the propensity of receiving help

Using 1552 individual breeding records between 1997 and 2002, we investigated how receiving help during a breeding attempt could be explained by individual-specific or environmental factors. In particular, in light of our initial results from generalized models on lifetime traits, we were interested in determining the causal factor(s) underlying the positive relationship between the propensity to receive help and a bird's lifespan. For this purpose, we performed logistic regressions to test whether receiving help during one breeding attempt was influenced by age, lifespan, brood number (birds had up to three broods in 1 year), year, feeding supplementation in this year or when nestling and interactions between these factors. A minimal model was reached after subsequently dropping the non-significant terms. This model was then extended to a generalized linear mixed model with nest box identity as a random effect, to investigate whether territorial quality could explain part of the variance in being helped when breeding. The importance of a nest box effect was assessed from the change in deviance when the factor was removed from the model, tested against a χ^2 distribution. Animal models including both individual and nest box as random effects did not converge, probably owing to insufficient sample size.

3. RESULTS AND DISCUSSION

Typically, most western bluebird breeding pairs are socially monogamous, but a small proportion (2–14%, Keyser *et al.* 2004) is assisted by helpers who feed the nestlings and defend the nest. Helpers are almost exclusively males and are usually related to the breeding pair; in our population of northwestern Oregon, we found 70% sons, 16% brothers, 6% daughters and 8% unrelated to the pair or of unknown relationship. The presence of helpers at a nest significantly increases reproductive success of the breeding pair (table 1; Dickinson & Akre 1998). However, from the helper's point of view, previous studies have shown that the fitness benefits of helping in western bluebirds do not compensate for failing to breed independently, even when taking into account hidden indirect or direct benefits from extra-pair fertilization (Dickinson & Akre 1998; Dickinson 2004b).

Table 1. Comparing lifespan and reproductive success in birds that received or did not receive help. (This analysis was restricted to 273 birds with at least one breeding that were recovered dead or had not been seen since 2000; significance (p) of the difference between the two classes is based on a two-tailed t -test.)

	n	average lifespan (s.e.)	average number of eggs laid per breeding attempt (s.e.)	average number of hatchlings per breeding attempt (s.e.)	average number of fledglings per breeding attempt (s.e.)	average number of recruits per breeding attempt (s.e.)
did not receive help	251	1.25 (0.03)	5.00 (0.05)	4.19 (0.09)	3.33 (0.11)	0.43 (0.04)
received help	22	1.86 (0.21)	5.31 (0.14)	4.73 (0.18)	4.12 (0.22)	0.78 (0.12)
p		0.004	0.031	0.009	0.001	0.008

Data over seven generations in this wild population of western bluebirds provided a unique opportunity to conduct pedigree-based quantitative genetic analyses in order to estimate heritabilities of helping and of being helped, after controlling for effects of sex, nestling food supplementation and lifespan. Using data on 1593 breeding individuals, we found that the narrow-sense heritability for being a helper for another pair's nesting attempt was 0.76 (s.e. = 0.25, figure 1), and the narrow-sense heritability for receiving help was 0.32 (s.e. = 0.13, figure 1). These results were confirmed by a simple threshold model which provided estimates of 0.74 and 0.23 for heritability of being a helper and receiving help, respectively, values well within the range of heritabilities estimated using an animal model approach. The two traits were positively phenotypically correlated (0.27, s.e. = 0.02), suggesting that a bird which was once a helper has a higher chance of being helped when breeding than a non-helper bird (15.4 versus 6.9%). The genetic correlation between the two traits was very high and not significantly different from one (1.00, s.e. = 0.19). We would expect a strong positive genetic correlation between being helped and helping, since a bird that passes a helping gene on to its offspring is likely to be helped by that offspring.

In a recent review on individual variation in social behaviour (Komdeur 2006), it was highlighted that behavioural ecologists have traditionally addressed the question of variation in cooperative breeding behaviour by studying the effects of environment factors but neglecting the study of a genetic component. This deficiency is due to the difficulty of obtaining sufficient quantitative data in most cooperative breeding species. Ours is the first quantitative genetic study showing heritability for the propensity to help or to receive help. Our finding complements a recent study showing heritability of parental effort in long-tailed tits (*Aegithalos caudatus*; MacColl & Hatchwell 2003). Taken together, these studies suggest that variation between individuals in the propensity to provide parental care as a parent or a helper does not arise solely from individuals making choices based on the estimates of current costs and benefits, but is, in part, heritable. Thus, rapid microevolutionary changes in the extent of cooperative breeding are possible. In particular, if analyses of fitness–trait relationships confirm that helping is associated with a high cost (i.e. a missed breeding opportunity), but with no indirect fitness benefits, we expect that cooperative breeding will gradually disappear in this population unless genetic correlations between helping behaviour and some other

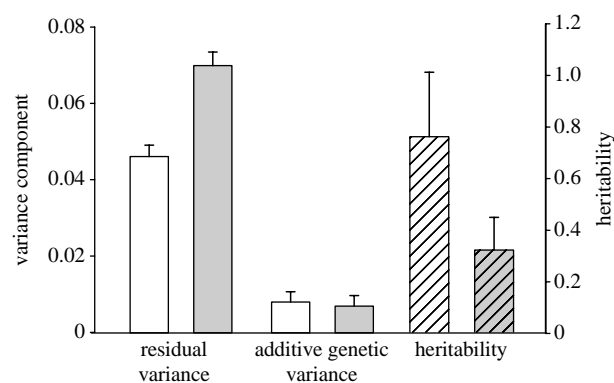


Figure 1. Estimates of variance components (left y -axis) and heritability on the liability scale (h^2_c , hatched bars, right y -axis) from an animal model quantitative genetic analysis of being a helper (white bars) and receiving help when breeding (grey bars). Vertical bars represent 1 s.e.

positively selected traits are sufficiently strong to maintain the low level of occurrence of helping.

Although we find strong evidence for heritability of helping behaviour, we do not yet know what mechanisms underlie this heritability. Whereas providing care to a brood as a helper clearly involves a set of behaviours with an underlying potential genetic basis (e.g. lower dominance and delayed dispersal), it is more difficult to envisage how birds can individually differ genetically in their propensity to receive help, as is suggested by the significant heritability found for this trait. One possibility is that an individual's behaviour can influence the chance of attracting helpers at a nest, depending, for example, on the level of aggressiveness it displays. Such behavioural strategies, now classically referred to as 'personality types', show strong genetic components in birds (e.g. Sih *et al.* 2004). Empirical studies are needed to compare personalities between birds which did or did not receive help when breeding, using standard laboratory tests. Another source of potential genetic variation in the propensity to attract helpers stems from the begging behaviour of the chicks in a nest. In the burrower bug, *Sehirus cinctus*, genetic variation was found for offspring elicitation of care as well as for maternal provisioning. These behaviours were also negatively genetically correlated (Agrawal *et al.* 2001), as predicted by parent–offspring conflict theory (Trivers 1972).

The patterns observed here could be due to the direct effects of individual genes or could arise from cultural inheritance. For example, helping behaviour could be learned and passed on non-genetically to relatives via social inheritance. Similarly, habitat quality has been

shown to be a major determinant in the decision to help rather than to attempt independent breeding (Komdeur 1992; Covas *et al.* 2004). If birds consistently breed in good-quality habitats and their offspring inherit these territories as breeding sites, then inheritance of territories could give rise to repeated patterns of helping within specific families. Box identity explained a significant part of the variance in receiving help ($n=1552$, change in deviance when removing from model is 84.06, χ^2 -test: $p<0.0001$), thereby illustrating the importance of environment effects in determining helping behaviour. Previous studies on western bluebirds have shown that helpers very often defend and attend nests within their natal territories (Kraaijeveld & Dickinson 2001; Dickinson 2004a). However, Dickinson (2004b) showed low potential for direct benefits of helping via territory inheritance. In our population, 5.5% of all breeders inherited their parent's nest box when breeding. When considering helpers only, this occurrence rises to 30%. This suggests that at least some, but not all, of the variation in the expression of helping behaviour could follow from the sharing of territories, calling for further work on the importance of territory quality on helping behaviour. However, a great advantage of using an animal model lies in the ability to simultaneously compare phenotypes of relatives related via a vast spectrum of routes through the pedigree (Kruuk 2004), thereby limiting the influence of cultural and common environment effects (territories are not shared by all distant relatives) and giving strong support for real additive genetic variance. To clearly distinguish genetic from cultural inheritance, future studies would need to carry out multigeneration cross-fostering experiments.

Thus far, we have shown that there is significant heritability for the probability of receiving help and that birds receiving such help lay more eggs, hatch more young, and produce more fledglings and more recruits than birds that do not receive help (table 1). However, we found no significant additive genetic variance for any of these lifetime fitness components (see electronic supplementary material) and the low sample size did not allow us to determine underlying genetic correlations between fitness traits and the propensity to receive help. Logistic regression analysis showed that the probability of receiving help during one breeding attempt depended on brood number (higher helping rate in second broods (7.6%) compared with first or third broods (4.0 and 4.6%)), and was positively correlated with the age of a bird and its total lifespan ($n=1552$, final model: brood, $F_{2,1547}=3.01$, $p=0.049$; age, $F_{1,1547}=14.17$, $p<0.001$; lifespan, $F_{1,1547}=4.36$, $p=0.037$). The positive relationship between probability of receiving help and lifespan is striking (figure 2) and holds over and above a simple age effect (see logistic regression results above): for a similar given age, birds with longer subsequent lifespan are more likely to be helped (figure 3). This suggests that either receiving help extends lifespan through a reduction in the costs of reproduction (Koenig & Dickinson 2004) or some unmeasured variable such as individual or territory quality is positively correlated with both lifespan and the probability of receiving help. The correlative approach does not allow us to distinguish these latter hypotheses. Interestingly, the correlation between lifespan and cooperative breeding that we find within the focal

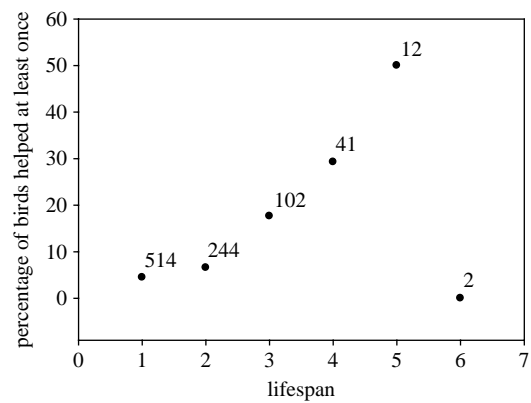


Figure 2. Percentage of birds that had help at least once when breeding, over their lifespan (number labels are sample sizes).

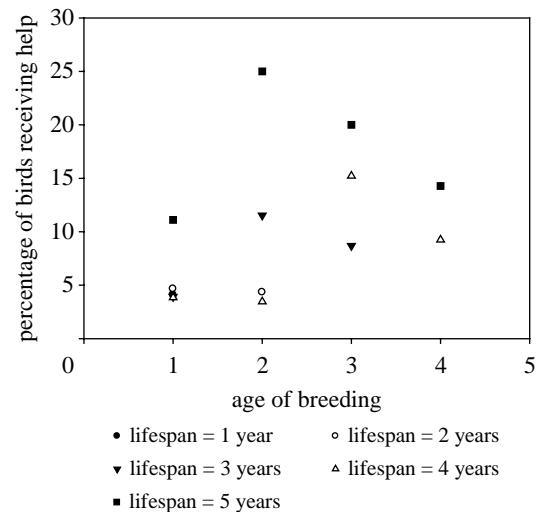


Figure 3. Combined effects of age and lifespan on the percentage of birds receiving help, using repeated values on birds over their lifetime. For birds of a given age, e.g. 3-year-old breeders, those with a subsequently longer lifespan receive more help.

population is consistent with patterns seen across species—long-lived species are more likely to exhibit cooperative breeding (Arnold & Owens 1998; although based on potentially biased estimates, see Cockburn 2003)—as predicted by Brown's (1987) 'life-history hypothesis' for cooperative breeding. This hypothesis states that species with lower mortality rates are more likely to evolve cooperative breeding owing to constraints on territorial availability. Hence, our results suggest that the macroevolutionary pattern observed between species could have arisen from microevolutionary processes operating within species.

To fully understand the evolutionary origin and present maintenance of social behaviour, we need to untangle the effects of genetics, environment and learning on a complex phenotype. In wild populations, the difficulty lies in monitoring multiple generations. In this, one of the first such studies, we have combined data from a long-term population study and powerful pedigree-based analyses to show that cooperative breeding behaviour has a heritable component. Clearly, ecological conditions also play a role in determining the propensity of an individual to help or be helped. Future work should elucidate the interplay between these two factors and the ultimate effect of cooperative breeding behaviour on fitness.

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