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PATERNAL CARE: DIRECT AND INDIRECT GENETIC EFFECTS OF FATHERS ON OFFSPRING PERFORMANCE

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Knowledge of how genetic effects arising from parental care influence the evolution of offspring traits comes almost exclusively from studies of maternal care. However, males provide care in some taxa, and often this care differs from females in quality or quantity. If variation in paternal care is genetically based then, like maternal care and maternal effects, paternal effects may have important consequences for the evolution of offspring traits via indirect genetic effects (IGEs). IGEs and direct–indirect genetic covariances associated with parental care can contribute substantially to total heritability and influence predictions about how traits respond to selection. It is unknown, however, if the magnitude and sign of parental effects arising from fathers are the same as those arising from mothers. We used a reciprocal cross-fostering experiment to quantify environmental and genetic effects of paternal care on offspring performance in the burying beetle, *Nicrophorus vespilloides*. We found that IGEs were substantial and direct–indirect genetic covariances were negative. Combined, these patterns led to low total heritabilities for offspring performance traits. Thus, under paternal care, offspring performance traits are unlikely to evolve in response to selection, and variation in these traits will be maintained in the population despite potentially strong selection on these traits. These patterns are similar to those generated by maternal care, indicating that the genetic effects of care on offspring performance are independent of the caregiver's sex.

KEY WORDS: **Cross-fostering, indirect genetic effects, maternal effects, parental effects, paternal care, quantitative genetics.**

Parental care is taxonomically widespread and is critical to the success and survival of offspring in many species (Royle et al. in press). In species with parental care, variation in the form, amount, and duration of care provided leads to variation in offspring survival, growth, and development. To date, research has primarily focused on the costs and benefits of parental care (Clutton-Brock and Godfray 1991; Royle et al. in press), and environmental influences of care on offspring fitness (Royle et al. in press), with considerably less work on how genetic variation in parental care is related to the expression of offspring phenotypes. This is despite the importance of the genetics of care for understanding the evolution of offspring traits (Walling et al. 2008). Although some of the variation in parental care behavior reflects random environmental effects, it is also often heritable (Hunt and Simmons 2002; Walling et al. 2008). Understanding how this heritable variation in parental care affects offspring phenotypes is essential to understanding how offspring traits will respond to selection.

If variation in parental care reflects genetic differences among parents (i.e., it is heritable), care may play an important role in the evolution of offspring phenotypes (Kirkpatrick and Lande 1989; Lande and Kirkpatrick 1990; Cheverud and Moore 1994; Mousseau and Fox 1998; Wolf et al. 1998). This is because

offspring inherit genes that affect both the phenotype of interest and the parental trait that influences this phenotype, meaning that the evolution of these two traits is not independent. Assessing the evolutionary importance of parental care on the expression of offspring performance traits requires consideration of both environmental and genetic influences over multiple generations (Cheverud and Moore 1994; Rauter and Moore 2002a). Parental care is influenced by both the environment to which the parent is exposed and the genes that are expressed in the parent. A parent's genes and environment indirectly affect offspring phenotype through their effects on parental care and may therefore operate as indirect genetic effects (IGEs) and indirect environmental effects, respectively (Cheverud and Moore 1994). In addition to parental care, offspring phenotype is also determined by the offspring's own genes (direct genetic effects) and the environment in which it is reared (direct environmental effects). The impact of these direct genetic and environmental effects may also depend on indirect genetic and environmental effects, as a result of correlations between direct genetic effects and IGEs as well as correlations between direct and indirect environmental effects (Cheverud et al. 1996; Lynch and Walsh 1998; Rauter and Moore 2002a). This correlation between direct genetic effects and IGEs is important because it can alter predictions of how traits respond to selection (Dickerson 1947; Kirkpatrick and Lande 1989; Cheverud and Moore 1994; Moore et al. 1997).

IGEs due to variation in parenting may influence the rate and direction of evolution of offspring performance through a covariance with direct genetic effects in the offspring (Cheverud and Moore 1994; Lynch and Walsh 1998; Wolf and Wade 2001; Bijma and Wade 2008). Empirical studies on the genetics of maternal care show that this covariance may sometimes be positive (e.g., red squirrels—McAdam et al. 2002; pigeons—Aggrey and Cheng 1995; great tits—Kölliker et al. 2000) or, more often, negative (e.g., mice—Falconer 1965; Riska et al. 1985; hogs—Dickerson 1947; Willham 1963; ungulates—Wilson and Réale 2006). The sign of this covariance is important as a positive covariance increases the total heritability and therefore the rate of evolution, whereas a negative covariance decreases total heritability and responses to selection, potentially reversing the direction of response (Dickerson 1947; Kirkpatrick and Lande 1989; Kirkpatrick 1992; Cheverud and Moore 1994; Moore et al. 1997; Bijma and Wade 2008). In addition, when IGEs are present, they may cause a time lag in response to selection (Kirkpatrick and Lande 1989; Lande and Kirkpatrick 1990; Kirkpatrick 1992; Wolf et al. 1999), because traits respond to selection operating on previous generations in addition to the current generation. As such, IGEs may allow for the evolution of traits that otherwise show no (direct) additive genetic variation. Predicting the evolution and phenotypic optimum of traits that are influenced by social environments therefore requires knowledge of the contributions of IGEs to genetic variance, and the sign and magnitude of the direct–indirect genetic covariance.

Previous studies investigating the role of IGEs on the evolution of offspring performance have focused exclusively on the role of maternal performance. However, in many species, males also (or alternatively) provide care (Ketterson and Nolan 1994; Balshine in press; Trumbo in press). In these species, paternal performance may be important in generating variation in offspring phenotypes. Whether the IGEs that arise from paternal care are the same as those that arise from maternal care is unknown. There is no a priori reason why maternal and paternal effects arising from care, and therefore IGEs, should be the same. Males and females often differ in the selection pressures that influence care, leading to differences in the way males and females care for offspring (Kokko and Jennions 2008). Such differences should result in differences in parent–offspring coadaptation depending on the sex of the parent (Wolf and Brodie 1998; Kölliker et al. 2005; Hinde et al. 2010). For instance, male effects are more likely to be exclusively postnatal in form whereas females often also contribute considerable prenatal effects through the egg (Mousseau and Fox 1998), and prenatal and postnatal effects have been shown to influence the evolution of parent–offspring coadaptation differently (Hinde et al. 2010). Furthermore, the nature of selection influences the form of parent–offspring coadaptation that is expected (Kölliker et al. 2005). If males and females show quantitative differences in the amount of postnatal care (even if both sexes provide all forms of care), such differences among the sexes may lead to different selection pressures that can limit the opportunity for coadaptation in males (Kölliker et al. 2005). Parent–offspring coadaptation is frequently observed in females across traits within parents (e.g., prenatal–postnatal coadaptation—Lock et al. 2007; Hinde et al. 2009), and across generations (e.g., parent–offspring coadaptation—Kölliker et al. 2000; Agrawal et al. 2001; Lock et al. 2004; Hinde et al. 2009). Coadaptation between fathers and offspring, however, has not been investigated.

Understanding how differences in the way the sexes invest in parental care impact offspring performance is not simply a theoretical problem; although studies on paternal effects are less common than those on maternal effects, there is increasing evidence that male contributions during rearing may be particularly important in determining offspring phenotypes (Qvarnström and Price 2001). For example, in a species of dung beetle, father–son resemblance in horn length is primarily determined by the level of paternal care provided not offspring genotype (Hunt and Simmons 2000) and in house sparrows badge size of sons more closely resembles care-giving fathers than biological fathers (Griffith et al. 1999). Thus, where these environmental influences of fathers and mothers differ and are genetically influenced, IGEs of males can differ from females.

Here, we investigate the evolutionary importance of IGEs on offspring growth and duration of development derived from uniparental male care in the burying beetle, *Nicrophorus vespilloides*. Burying beetles provide an ideal system for studying these questions as both sexes exhibit extensive and flexible care of offspring (Eggert and Müller 1997; Scott 1998). Male and/or female *N. vespilloides* bury a small carcass that constitutes a food resource for developing offspring and continue to provide direct (regurgitation of food to the begging offspring) and indirect (preparation and maintenance of the carcass) care throughout larval development. Although males and females can perform all parental tasks, during biparental care the sexes usually have different roles. Females tend to provide more direct care than males (Smiseth and Moore 2004; Smiseth et al. 2005; Walling et al. 2008) and duration of care is shorter and more variable in males than females (Bartlett 1988). Females are more likely to provide uniparental care than males (39% for females, 3% for males; Eggert 1992), but when males do care alone they provide nearly identical levels of care as females (Smiseth et al. 2005; Walling et al. 2008). In addition, burying beetles are amenable to quantitative genetic studies. There is underlying genetic variation in all parental care behaviors for both sexes in *N. vespilloides* with moderate to strong intersexual genetic correlations (Walling et al. 2008). However, within the sexes, the pattern of genetic correlations between parental care behaviors differs for males and females. Thus, the genetic architecture of parental care behavior and selection on care behavior suggests sex-specific lines of least evolutionary resistance (Walling et al. 2008). These results suggest that the way in which maternal and paternal care affect offspring performance is likely to be different. Furthermore, IGEs arising from females have been estimated and maternal effects are well-studied in burying beetles (*N. pustulatus*—Rauter and Moore 2002a,b; and *N. vespilloides* – Lock et al. 2004, 2007).

We use a reciprocal cross-fostering breeding design (Lynch and Walsh 1998) to determine the importance of paternal performance arising from uniparental male care in causing variation in offspring size and development time in *N. vespilloides*. We randomly paired males with a female then removed the female after egg-laying so the males reared young alone, and reciprocally exchanged half of the offspring from each family with half of the offspring from another family. Such an experimental design allows us to partition the phenotypic variance in offspring traits into direct genetic effects, IGEs arising from paternal performance, the covariance between direct genetic effects, and IGEs of paternal performance while experimentally controlling other environmental influences. We expect that IGEs due to variance in paternal care that we estimate here will be lower than estimates for maternal care from previous studies due to the decreased opportunities for coadaptation and selection on care performed by fathers. Also, we predict that the effects of paternal care will be greatest for early-life traits and will diminish as offspring age, as has been found for parental effects arising from maternal care (Cheverud and Moore 1994).

Methods

STOCK MAINTENANCE

Our stock population originated from 60 male and 60 female *N. vespilliodes* caught in Devichoys Wood, Cornwall, UK (N50°11′47″E5°7′23″) in July, 2010. Beetles were trapped using Japanese beetle traps baited with salmon. An outbred stock population was maintained by breeding 50–60 random pairs per generation. Each beetle was only used in one breeding attempt per generation. To breed, a pair of virgin male and female beetles was placed in a breeding chamber (i.e., a transparent plastic container: 17 × 12 × 6 cm) filled with 2 cm of moist soil and a 15–25 g mouse carcass (Livefoods Direct, Sheffield). Larvae dispersing from these carcasses were removed from the breeding chamber and placed in individual rearing containers (clear plastic container: 7 × 7 × 4 cm) filled with 2 cm of moist soil. After eclosion, beetles remained in these individual containers and were fed two decapitated mealworms (*Tenebrio*) twice a week. All rearing was conducted in a constant temperature room at 21 ± 1°C with a 16L:8D light regime. Our experiments were run in three blocks, using generations four to seven of this laboratory stock. We statistically controlled for this block effect (see below).

EXPERIMENTAL DESIGN

To create families for cross-fostering, we mated randomly paired virgin males and females taken from our laboratory stock. We placed the pair in a clear plastic breeding box (17 × 12 × 6 cm) with a freshly defrosted mouse carcass (18.0–20.0 g) and filled with 2 cm of moist soil. After pairing, breeding boxes were kept in an incubator with the same temperature and light cycle as in the laboratory. Breeding boxes were checked for eggs three times a day (approximately every 8 h). Twenty-four hours after the first eggs in a box were noted we removed the female and transferred the male and carcass to a new breeding box. The old breeding box with the eggs was placed together with the new breeding box containing the male and carcass back into the incubator. The eggs were then monitored three times a day for hatching larvae.

Once larvae began to hatch, we paired families to establish each reciprocal cross-fostered unit. Families were matched according to the onset of hatching and number of larvae hatching. Within each cross-fostered pair, 7–10 offspring from each family were added to the carcass of each parental male. Thus, within each pair, each father raised 7–10 of his own (biological) offspring together with the same number of unrelated (foster) offspring, so that each male raised a total of 14–20 offspring. The number

of offspring added to the carcass in our experiment is within the range that single male parents are capable of rearing on this size carcass (Walling et al. 2008) and within the range that a single parent can rear in the wild (Müller et al. 1998). We added larvae to each carcass over a 24-h period, because larvae within families hatched asynchronously over this time period. For each pair of cross-fostered families, we ensured that we always added the same number of larvae from each family to both carcasses at the same time. To allow us to identify the family from which larvae originated, we marked newly hatched larvae by cutting off the tip of either the left or right hind tarsus, using a scalpel. This method of larval identification has been used previously and does not affect larval survival or growth (Rauter and Moore 2002a). This marking method minimally affects pupation time (Rauter and Moore 2002a); however, this should not bias our results as all larvae were marked. All offspring received paternal care only. This breeding design resulted in 45 cross-fostered pairs and 1672 offspring in total.

OFFSPRING PERFORMANCE MEASURES

Seventy-two hours after the first larvae were placed on a carcass, we weighed all larvae individually to the nearest 0.1 mg. We determined the onset of larval dispersal by inspecting all breeding boxes three times a day. Larvae were classed as dispersing when at least two larvae had left the carcass and were wandering around on the surface of the soil or were buried in the soil away from the carcass. At dispersal, we counted the number of biological and foster larvae surviving from hatching to dispersal for each carcass and weighed all larvae individually to the nearest 0.1 mg.

Once larvae dispersed, we placed them in individual rearing containers (7 × 7 × 4 cm) filled with 2 cm of moist soil. To determine the duration of the wandering phase, we monitored these containers two times per day (approximately every 12 h). The end of the wandering phase and beginning of pupation was recorded as the time when a larva remained in the same position in the container for at least two consecutive observations. Thirteen days after the onset of pupation, each container was checked twice a day for newly eclosed adult beetles, which were weighed to the nearest 0.1 mg. We measured pronotum width (a widely used and accurate surrogate measure of size; (Beeler et al. 1999) of all newly emerged beetles to the nearest 0.1 mm using calipers. We also recorded the sex and survival of beetles from hatching to eclosion (i.e., emergence of adults from pupae).

STATISTICAL ANALYSIS

Performance of biological and foster offspring

To investigate whether male *N. vespilloides* treated larvae differently during parental care, we used paired *t*-tests to look for differences between biological and foster larvae in offspring performance within families. If fathers control investment toward offspring and there is coadaptation between fathers and their offspring, based on theoretical work (Kölliker et al. 2005; Hinde et al. 2010) we predicted that biological larvae would have greater survival, size, and/or shorter development times than foster larvae.

Estimation of genetic parameters

We estimated variance components of the observed phenotypic variation from a series of ANOVAs using the methods outlined by Riska et al. (1985). This method employs a mixed model approach specifically designed for the analysis of reciprocal cross-fostering breeding designs and is particularly efficient at isolating variance due to IGEs using estimates from related and unrelated individuals and shared and unshared environmental (parenting) effects in all possible combinations. The method of calculation of the various covariances that can be generated from our experimental design, and the interpretation of these components, is given in Table 1. The method makes use of the fact that cross-fostering within a known breeding design yields multiple types of experimental combinations that can be analyzed in a series of hierarchical ANOVAs producing different types of observational components of variance (Table 1; Riska et al. 1985). Given these expectations, these components can then be combined in specific linear combinations to generate variances and covariances, as defined in Table 2.

Similar to nearly all previous cross-fostering studies of maternal effects (Riska et al. 1985; Rauter and Moore 2002a,b), we used full sibling. The use of full siblings (and the fact that our cross-fostering treatment occurred after larval hatching) means that variation due to prenatal maternal effects is allocated to dominance genetic variation. Although dominance deviations are partitioned out of the estimate of the direct genetic variances, they remain confounded with the indirect genetic variances, potentially biasing estimates of indirect heritabilities. It is not possible to determine the extent or direction of this bias, especially as indirect dominance effects are rarely estimated. However, there is little evidence that maternal investment in eggs has long-term effects on variation in offspring performance in burying beetles (Rauter and Moore 2002a,b). Moreover, because it is estimated from components derived from different ANOVAs, our estimate of the direct–indirect covariance is unaffected by this potential bias (Table 1).

Unlike previous studies using this method (e.g., Riska et al. 1985; Gleeson et al. 2005), we did not have measures of parental phenotypes. Because of this, we could not estimate all potential contributions to variation in offspring traits (Lynch and Walsh 1998). As a result, our measures correspond to observational components 5–10 in Riska et al. (1985). Component 5 (9 in Riska et al. 1985) was calculated using the corrected method described in later

Table 1. Calculation of components of variation for six types of relatives, along with the specific covariance that is estimated.

Observed component (Y_i)	Covariance	Method for estimation
Y_1	Covariance between full siblings raised by their genetic sire	Estimated from the carer term of the ANOVA with carer nested within pair (only using data when sire and carer are the same, i.e., only genetic offspring)
Y_2	Covariance between unrelated sibling where the offspring were cared for by an unrelated sire	Estimated from the carer term of the ANOVA with carer nested within pair (only using data when sire and carer are not the same i.e. only foster offspring)
Y_3	Covariance between full siblings raised by different carers	Estimated from the sire term of the ANOVA with carer nested within sire within pair, ignoring the identity of carers between sires (i.e., carers coded 1 and 2 within sires)
Y_4	Covariance between unrelated sibling, raised by the same carer	Estimated the carer term of the ANOVA with sire nested within carer within pair, ignoring the identity of sires between carers (i.e., sires coded 1 and 2 within carers)
Y_5	Covariance between unrelated sibling, each cared for by the others genetic sire	$Y_1 - Y_2$
Y_6	Variance among full siblings all with the same carer	Estimated from the error variance from the ANOVA for Y_3 or Y_4

Definitions modified from Riska et al. (1985). Further details provided in methods.

publications using the Riska et al. method (McAdam and Boutin 2003; Gleeson et al. 2005).

Variances for each observational component were estimated as outlined in Riska et al. (1985):

$$\mathrm{VAR}(\sigma^2) = \frac{(2\mathrm{MS}^2)}{\mathrm{df} + 2}$$

in which MS represents the mean square of the term of interest and df is the corresponding degrees of freedom.

We assessed the impact of the genetic and environmental contributions to offspring phenotype, and thus the potential for evolution of a specific trait, by comparing the proportions of the phenotypic variation accounted for by each factor. For direct genetic effects, we calculated the direct heritability ($h_O{}^2$) for each trait as

$$h_O^2 = \frac{\sigma_{AO}^2}{\sigma_P^2}$$

where σ_{AO} is the additive genetic variance and σ_P is the total phenotypic variance. For IGEs, we calculated the indirect heritability arising from effects of the care of the father ($h_F{}^2$) as

$$h_F^2 = \frac{\sigma_{AF}^2}{\sigma_P^2}$$

where σ_{AF} is the variance due to differences in paternal performance. To standardize the genetic covariance between direct genetic effects and IGEs, we calculated the genetic correlation between direct genetic effects and IGEs as

$$r_{(AO,AF)} = \frac{\sigma_{AOAF}}{\sqrt{\sigma_A^2 \times \sigma_F^2}}$$

where σ_{AOAF} is the covariance between direct genetic effects and IGEs. Total heritability was calculated as

$$h_T^2 = \frac{\left(\sigma_{AO}^2 + 0.5\left(\sigma_{AF}^2\right) + 1.5(\sigma_{AOAF})\right)}{\sigma_P^2}$$

following Willham (1972). Standard errors of the heritabilities and genetic correlations were calculated using the methods for full-sibling SE outlined in Falconer and Mackay (1996).

Controlling for factors other than paternal performance

Several environmental factors, in addition to parental performance, can have effects on offspring growth and development. These factors include mass of the mouse carcass, brood size, birth order, age of parents, and sex of the offspring (Smiseth and Moore 2002, 2004; Smiseth et al. 2006; Lock et al. 2007; Gibbs et al. 2008). Brood size, which reflects resource availability and genetic influences of parents (Smiseth and Moore 2004; Walling et al. 2008), also influences male and female parental care differently

Table 2. Design matrix (X) displaying theoretical causal components of the observed covariances.

Observed component	Causal components					
	σ^2_{AO}	σ^2_{DO}	σ_{AOAF}	σ^2_{AF}	σ^2_{DF+C}	σ^2_{E}
Y_1	0.5	0.25	1	1	1	0
Y_2	0.5	0.25	0	1	1	0
Y_3	0.5	0.25	0.5	0	0	0
Y_4	0	0	0.5	1	1	0
Y_5	0	0	1	0	0	0
Y_6	0.5	0.75	0	0	0	1

σ^2_{AO}, additive direct genetic variance; σ^2_{DO}, dominance direct genetic variance; σ_{AOAF}, direct–indirect (paternal) genetic covariance; σ^2_{AF}, additive indirect (paternal) genetic variance; σ^2_{DF+C}, dominance indirect (paternal) genetic variance + common environmental variance; σ^2_{E}, residual environmental variance.

(Smiseth and Moore 2004). Because these factors were controlled in previous studies of indirect genetic influences arising from maternal care (Rauter and Moore 2002a,b; Lock et al. 2004, 2007), we controlled them here to clarify paternal IGEs under standard conditions and to facilitate comparisons with previous studies. We also ran our experiment in three blocks to ensure sufficient sample sizes. Therefore, we controlled these factors both experimentally and statistically to allow variation in offspring phenotypes to be accurately partitioned into genetic and nongenetic components.

Variation in the number of offspring and resource quantity was reduced by limiting the total number of offspring added to a carcass to between 14 and 20, always with an equal number of biological and foster offspring, and by only using mice between 18 and 20 g in mass. To assess the effectiveness of these controls, we looked at the correlations between each of these factors and our offspring performance measures. We found only one significant (but weak) correlation (out of eight), between mouse mass and any measure of offspring performance (total development time: $r_{89} = -0.238$, $P = 0.024$), demonstrating the effectiveness of our experimental controls.

Other factors including block, number of larvae dispersing from the carcass, and sex of offspring (once offspring identity could be tracked) were controlled for statistically by using the residuals from the regression of each offspring performance measure on these factors in our genetic analyses. Data have been deposited in the Dryad repository: doi:10.5061/dryad.8906j.

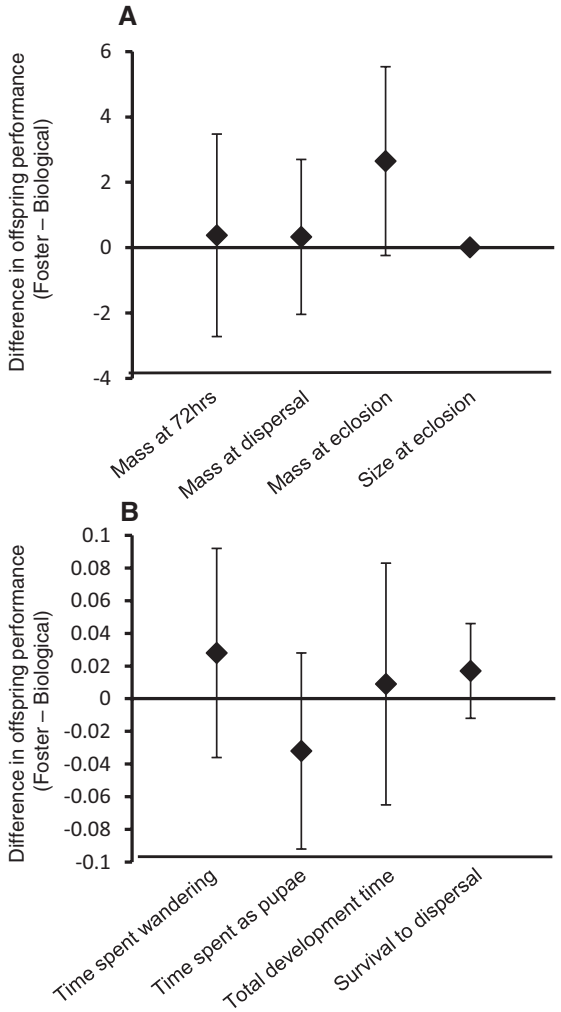

Figure 1. Difference in phenotypic mean of foster and biological offspring for each of the offspring performance measures (± SE), $N = 89$ social families. Biological and foster offspring means did not differ for any of the performance measures. (A) Offspring size: mass (mg) 72 h after larvae placed on carcass ($t_{(87)} = 0.122$, $P = 0.903$), mass (mg) when larvae disperse from carcass ($t_{(87)} = 0.139$, $P = 0.890$), mass (mg) at eclosion ($t_{(87)} = 0.917$, $P = 0.362$), and pronotum width (mm) at eclosion ($t_{(87)} = 0.375$, $P = 0.708$). (B) Development time and survival: time (days) spent in the wandering stage ($t_{(87)} = 0.436$, $P = 0.664$), time (days) spent in the pupal stage ($t_{(87)} = -0.523$, $P = 0.602$), total development time (days) from hatching to eclosion ($t_{(87)} = 0.123$, $P = 0.902$), proportion of larvae surviving to dispersal ($t_{(87)} = 0.224$, $P = 0.823$).

Results

PERFORMANCE OF BIOLOGICAL AND FOSTER OFFSPRING

There were no statistically significant differences in the effects of fathers on biological or foster offspring in any of our offspring performance measures (Fig. 1; all Ps > 0.362). General patterns were consistent with previous findings when females care for offspring. Larval growth occurred primarily in the first 72 h, which corresponds to the period of maximum care. Once they dispersed from the carcass, larvae stopped growing and began wandering to find a site for pupation. This wandering phase was short (four to six days) and was followed by the pupal stage that lasted

14–15 days for both treatments. The phenotypic variance differed only for one offspring performance trait (time spent in the pupal stage) depending on whether the offspring were reared by biological or foster fathers. Foster larvae showed greater variation in time spent in the pupal stage than did biological larvae (Levene's test: $P < 0.001$). All other phenotypic variances did not differ for biological and foster offspring (Levene's test: $P > 0.117$)

GENETIC PARAMETERS

Estimates of the genetic variances and covariances contributing to offspring performance are presented in Table 3, with the corresponding heritabilities and genetic correlations presented in Table 4. Parameter estimates for direct and indirect genetic influences on offspring size measures show an ontogenetic pattern and substantial IGEs. For our early measure of mass at 72 h, which corresponds to the point at which parental care begins to wane, there was little evidence of a direct genetic effect, but substantial IGE. Subsequent measures of mass, at dispersal and after eclosion, and size at adult emergence show high direct heritability and high to moderate indirect heritability. This result suggests that the relative importance of IGEs lessens through ontogeny with a corresponding increase in the importance of direct genetic effects. The direct–indirect genetic correlation was negative for all measures of mass and size. The presence of strong negative direct–indirect genetic correlations means that the total heritability was low or even negative for all traits, suggesting a genetic constraint on further evolution.

Our measures of development time show a different pattern to that of offspring size. We found negligible direct heritabilities for both developmental stages we measured. The indirect genetic heritability was moderate for both, and a moderate direct–indirect genetic correlation for time spent wandering. The genetic correlation for duration of the pupae could not be calculated due to negative direct genetic variance component. Total heritability was again low or negative.

Almost all observed components contributing to the variance in the genetic parameters were highly significant (Table 5). The exception to this is component 7, which only had a significant contribution to offspring mass at eclosion.

Discussion

Despite the prominent role that fathers play in providing parental care in many species across a broad range of taxa (Balshine in press; Trumbo in press), and the importance of quantifying genetic variation to understand how parental care traits evolve (Walling et al. 2008; Kölliker et al. in press), there are few studies on the contribution of paternal care to the evolution of offspring performance from a quantitative genetic perspective. Here, we present the first study that explicitly sets out to partition variance in offspring performance measures to direct and indirect genetic components when males provide care for their offspring. There are several key findings. First, we found offspring performance did not depend on whether it was the biological father or the foster father providing care, which suggests that in *N. vespilloides* fathers, in contrast to mothers, do not control investment in offspring. Second, similar to patterns for maternally derived IGEs, we found the relative importance of IGEs arising from paternal care depends on ontogenetic effects and the characteristics of the specific trait being examined. Third, as has most frequently been found for maternal effects, the correlation between direct–indirect genetic effects (where present) was strong and negative. This negative correlation is likely to restrict how offspring performance traits respond to selection and be important in maintaining genetic variation. Finally, we found little difference in the contributions of IGEs on offspring performance arising from paternal care (our study) compared to those arising from maternal care (Wilson and Réale 2006). Combined, these results indicate that, under uniparental care, the influence of burying beetle fathers via indirect genetic contributions to offspring performance is consistent with the pattern of contributions of mothers in species with parental care.

Biological and foster offspring did not differ in performance, suggesting fathers do not control investment toward offspring and that there is no coadaptation between paternal care and offspring begging. This result contrasts with a previous study on maternal care in *N. vespilloides* (Lock et al. 2004), which showed that mother's provisioning and offspring begging are coadapted, with a positive genetic covariance between these traits that leads to increased offspring fitness when raised by their biological mother. This difference between mothers and fathers in coadaptation with offspring may reflect differences in selection on care by the two sexes. In contrast to females, males are more flexible in the amount of care they provide, adjusting it to the presence or absence of the female (Smiseth et al. 2005) and to the number of offspring begging (Smiseth and Moroe 2004). Walling et al. (2008) also suggest that female care is under directional selection but male care is not. Variable coadaptation between parents and offspring is further supported by differences between studies on burying beetle species that differ in the nature of maternal care. In contrast to *N. vespilloides*, *N. pustulatus* shows no evidence for mother-offspring coadaptation (Rauter and Moore 2002a). *Nicrophorus pustulatus* is unusual for a burying beetle because offspring can develop with no parental care at all (Rauter and Moore 2002b). *Nicrophorus vespilloides* on the other hand, is an obligate carer, and females almost always provide care either as sole carer, or primary carer, in biparental situations (Eggert et al. 1998). Combined, these studies showing sex and species differences in coadaptation support the idea that rarity of parental care limits the evolution of coadaptation and that coadaptation between parental

Table 3. Variances and covariances derived from linear combinations of hierarchical ANOVA components.

Offspring performance trait	σ^2_{AO}	σ^2_{DO}	σ_{AOAF}	σ^2_{AF}	σ^2_{E}
Mass at 72 h[1]	72.69	186.94	−220.92	623.04	753.10
Mass at dispersal[1]	94.00	134.73	−168.44	337.59	172.48
Mass at eclosion[1]	258.66	8.88	−223.41	284.01	239.82
Size at eclosion[2]	241.16	3.21	−338.28	311.46	325.15
Time spent wandering[3]	323.81	706.58	−146.90	1441.36	5283.52
Time spent as pupae[3]	−45.82	567.43	−1513.70	1672.14	3320.29

[1]Measured in mg.
[2]Measured in mm.
[3]measured in days.

Table 4. Genetic parameters. Direct heritability (h_O^2), indirect heritability (h_F^2) due to differences in paternal performance, the direct–indirect genetic correlation ($r_{(AO,AF)}$), and the total heritability (h_T^2) ± SE for each of the offspring performance traits measured.

Trait	h_O^2	h_F^2	$r_{(AO,AF)}$	h_T^2
Mass at 72 h[1]	0.07 ± 0.03	0.43 ± 0.08	–1.04 ± 0.22	−0.09 ± 0.02
Mass at dispersal[1]	0.20 ± 0.05	0.56 ± 0.10	–0.94 ± 0.02	0.07 ± 0.02
Mass at eclosion[1]	0.37 ± 0.08	0.36 ± 0.08	–0.82 ± 0.05	0.10 ± 0.03
Size at eclosion[2]	0.31 ± 0.07	0.35 ± 0.08	–1.23 ± 0.23	−0.12 ± 0.01
Time spent wandering[3]	0.05 ± 0.03	0.20 ± 0.05	–0.22 ± 0.26	0.01 ± 0.04
Time spent as pupae[3]	0.00 ± 0.02	0.34 ± 0.07	N/A[4]	−0.36 ± 0.05

[1]Measured in mg.
[2]Measured in mm.
[3]measured in days.
[4]The direct-indirect genetic correlation for time spent as pupae cannot be calculated due to a negative additive direct variance.

care and begging may be limited to species or parents with obligate care. The specifics of coadaptation between male care and offspring deserve further investigation.

Given this lack of a coadaptation between paternal care and offspring begging, we expected to see lower IGEs associated with paternal care than those associated with maternal care but this was not the case. Similar to studies on IGEs due to maternal care (Wilson and Réale 2006), we found direct and indirect heritabilities for offspring size measures under paternal care were moderate in magnitude. Although we found little evidence for direct genetic effects on development time arising from paternal care in *N. vespilloides*, previous studies on *Drosophila* spp. (reviewed in Roff and Mousseau 1987) indicate that heritability of development time may be highly variable both within and between studies. Also consistent with the majority of studies of direct–indirect covariances in animals with maternal care, we found strong negative correlations between direct genetic effects and IGEs for offspring size traits, which are expected to result from genes having antagonistic pleiotropic effects on parental performance and offspring traits (Wilson and Réale 2006). This lack of difference between IGEs resulting from maternal and paternal care suggests that differences between the sexes in the potential for coadaptation across traits within individuals and across generations may not be important in determining the strength of IGEs. The generality of our results to other species with paternal care, however, is currently unknown.

The presence of a negative correlation between direct genetic effects and IGEs can have important consequences for the evolution of offspring traits. Negative correlations between these genetic effects reduce total heritability (Table 3) and may thereby limit the potential response of offspring size to selection. This constraint means that, even in the face of strong selection on body size (as is expected for life-history traits Roff 2002), direct genetic variation for this trait will be maintained. Therefore, even though size is an important trait influencing adult fitness through both male–male and female–female competition for resources (Bartlett and Ashworth 1988; Otronen 1988; Müller et al. 1990), it may remain genetically and phenotypically variable because of the observed negative covariance between direct genetic effects and IGEs.

As predicted, we also found that the relative importance of paternal effects on offspring phenotype decreased with ontogeny. This is again similar to studies on maternal effects (Wilson and Réale 2006). Such ontogenetic patterns have been suggested to

Table 5. Significance of observed components from ANOVAs used to estimate contributions to the variance estimates.

Trait	Component	df	MS	*F*	*P*
Mass 72 h					
	Y_1	45	4011.187	4.718	0.000
	Y_2	44	5519.623	6.656	0.000
	Y_3	45	3173.431	0.912	0.627
	Y_4	45	6225.860	3.251	0.000
	Y_5[1]	44	−1508.44		
	Y_6[1]	1052	839.626		
Mass at dispersal					
	Y_1	44	2114.578	6.928	0.000
	Y_2	44	3102.603	10.487	0.000
	Y_3	45	2146.621	1.315	0.137
	Y_4	44	2962.527	2.508	0.000
	Y_5[1]	43	−988.025		
	Y_6[1]	960	300.848		
Mass at eclosion					
	Y_1	43	2076.674	4.598	0.000
	Y_2	44	3396.336	7.707	0.000
	Y_3	45	2679.492	1.708	0.016
	Y_4	44	2783.984	1.881	0.006
	Y_5[1]	43	−1319.7		
	Y_6[1]	960	446.104		
Pronotum width					
	Y_1	43	1854.189	3.110	0.000
	Y_2	44	3805.515	7.291	0.000
	Y_3	45	2631.104	1.402	0.089
	Y_4	44	3132.786	1.971	0.003
	Y_5[1]	43	−1951.300		
	Y_6[1]	960	558.577		
Time spent wandering					
	Y_1	43	14516.7	2.624	0.000
	Y_2	43	15488.4	2.815	0.000
	Y_3	45	13223.4	1.161	0.272
	Y_4	43	16528.3	1.669	0.021
	Y_5[1]	43	−971.66		
	Y_6[1]	934	5517.71		
Time spent as pupae					
	Y_1	43	7169.556	2.127	0.000
	Y_2	43	17107.574	4.040	0.000
	Y_3	45	777.41	0.717	0.890
	Y_4	43	16189.065	2.717	0.000
	Y_5[1]	43	−9938.018		
	Y_6[1]	934	3808.232		

[1]Components 5 and 6 do not have associated significance values because of the way they are calculated (see methods and Table 1).

be the result of "compensatory" or "targeted" growth (Cheverud et al. 1996), where multiple growth trajectories lead to the same ultimate phenotype. The fact that this pattern persists regardless of whether care is provided by males or females suggests that it is not driven by the effects of prenatal care or coadaptation between offspring and their mothers. From an offspring's perspective, under uniparental conditions, mothers and fathers are equivalent to each other.

In addition to parental care, IGEs may also operate via prenatal mechanisms (Bonduriansky and Head 2007). For instance, females can influence offspring phenotype prenatally via resource allocation toward eggs or embryos (Mousseau and Fox 1998),

whereas males may transfer substances via the ejaculate during mating that are either incorporated into the egg directly, or influence how females allocate resources to fertilized eggs (Ram and Wolfner 2007; Curley et al. 2011). In *N. vespilloides*, prenatal maternal effects interact with postnatal maternal effects to influence offspring synergistically due to a coadaptation between the two (Lock et al. 2007). Although our experimental design precludes assessment of such prenatal effects arising from male contributions, differences between how prenatal maternal and paternal effects operate (Demuth and Wade 2007) may lead to differences between the sexes in how IGEs influence offspring phenotypes. This would be an interesting avenue for future investigation.

One unanswered question that arises from our study is how care in a uniparental context reflects paternal effects expected under biparental care. Burying beetles are unusual in that they exhibit female uniparental care, male uniparental care, and biparental care with apparently little or no fitness differences associated with the different forms of care (Eggert and Müller 1997; Scott 1998). Male-only care is relatively rare, but there are strong genetic correlations between the expression of care behavior by males and females (Walling et al. 2008). Also, although the sexes both express all forms of care behavior, males and females differ in the amount of time spent performing different care behaviors during biparental care (Smiseth and Moore 2004; Smiseth et al. 2005; Walling et al. 2008). This partitioning of labor may mean that the genetic effects of paternal and maternal care differ depending on whether they are expressed during bi- or uniparental care. Furthermore, the genetic effects arising from maternal and paternal uniparental care may no longer be similar under biparental care. Exactly how the genetic effects of parental care under biparental care are likely to differ from uniparental care is difficult to predict, and future studies should address this question.

Conclusions

Researchers are becoming increasingly aware of the importance of social environments in contributing to genetic variation, and therefore evolution, via IGEs (Moore et al. 1997; Wolf et al. 1999; Bijma and Wade 2008; Bleakley and Brodie 2009; McGlothlin et al. 2010). The genetic variation contributed by social environments, in this case the social environment provided by fathers, can affect total heritability, and therefore the rate and direction of the evolution of offspring traits. Parental care, which is taxonomically widespread, often genetically variable and clearly important for offspring performance and fitness, is a major source of IGEs (Cheverud and Moore 1994; Rauter and Moore 2002a). A more complete understanding of the evolutionary consequences of parental care therefore depends on knowledge of genetic variation in care, and the extent that care contributes IGEs to offspring performance. Despite this, there are very few studies that have measured IGEs arising from parenting, particularly the direct–indirect genetic covariance, and none that attempt to determine whether males and females differ in their contribution to offspring performance via IGEs.

Our results suggest that paternal care, like maternal care, provides an important source of IGEs that may affect the evolution of offspring performance traits in *N. vespilloides*. For many of our offspring performance traits, we found substantial IGEs, as well as negative direct–indirect genetic covariances. These effects combine to give low estimates of total heritability for offspring performance, which means that these traits are unlikely to respond to selection and their evolution is thus constrained by the presence of IGEs (when males provide care alone). Our results also indicate that under uniparental conditions, IGEs associated with paternal care are similar to those arising from maternal care. This is despite differences in the potential for coadaptation between offspring and their mothers and fathers. Further studies should explicitly examine whether coadaptation facilitates the evolution of offspring performance as well as investigate how paternal and maternal effects contribute to the evolution of offspring traits under conditions of biparental care.

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