Niche variation and the maintenance of variation in body size in a burying beetle

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Abstract. 1. In burying beetles (Nicrophorinae), body size is known to provide both a fecundity advantage (in females) and successful resource defence (in males and females). Despite this, considerable variation in body sizes is observed in natural populations.

2. A possible explanation for the maintenance of this variation, even with intra- and inter-specific resource competition, is that individuals might assort according to body size on different-sized breeding resources.

3. We tested prediction that 'bigger is always better', in the wild and in the laboratory, by experimentally manipulating combinations of available breeding-resource size (mouse carcasses) and competitor's body size in *Nicrophorus vespilloides* (Herbst 1783).

4. In the field, large female beetles deserted small carcasses, without breeding, more often than they did larger carcasses, but small females used carcasses indiscriminately with respect to size. In the laboratory, large beetles reared larger broods (with more offspring) on larger carcasses than small beetles, but on small carcasses small beetles had a reproductive advantage over large ones. Offspring size covaried with carcass size independently of parental body size.

5. The present combined results suggest breeding resource value depends on an individual's body size, and variation in body size is environmentally induced: maintained by differences in available carcass sizes. This produces a mechanism by which individual specialisation leads to an increase in niche variation via body size in these beetles.

Key words. Body size, individual specialisation, niche variation, non-genetic inheritance.

Introduction

Benefits of a large body size have been observed across a wide range of taxa. Common benefits include increased fecundity (Darwin, 1871; Shine, 1988; Roff, 2002), and an advantage in competition for breeding resources or mating opportunities (Andersson, 1994; Blanckenhorn, 2005). Although resource competition typically favours larger individuals within species, size differences among species may also be maintained when individuals of different species compete for resources resulting in inter-specific niche partitioning (MacArthur & Levins, 1967;

Roughgarden, 1974). Morphologically similar or closely related species may persist in a community and share the same range if they use different resource classes or if they segregate by size and each exploits resources at different positions along an axis of resource variation (e.g. a habitat characteristic, prey size, etc.) (Schoener, 1974; Werner & Gilliam, 1984). A related inverse scenario, the niche variation hypothesis, predicts that when competition between species is relaxed, a population may become more generalised via individual specialisation (Bolnick *et al.*, 2007). In this case, individual resource-use specialisation can result in the niche width of a population being much broader than the niche width of each individual (Roughgarden, 1974; Violle *et al.*, 2012).

Intra-specific competition is one mechanism that might drive individual resource-use specialisation, for example, if subdominant or smaller individuals are relegated to alternative or inferior

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quality resources (Morse, 1974; Araújo *et al.*, 2011). In this way, niche variation could increase whether or not there was a single body size optimum. However, individuals may also have different preferences or functional limitations related to certain phenotypes (e.g. biomechanical trade-offs) that prevent optimal exploitation of all available resource classes, potentially leading to disruptive selection (Van Valen, 1965; Bolnick *et al.*, 2003; Ackermann & Doebeli, 2004). A classic example is the medium ground finch, *Geospiza fortis* (Gould 1837), in which variation among individuals in bill morphology determines the efficiency with which birds can handle seeds from different plant species leading to individual dietary specialisation (Price, 1987).

Studies in vertebrates support the idea that populations might become more generalist via niche variation among individuals (e.g. see Bolnick *et al.*, 2007). However, studies examining individual niche variation in insects are rare despite evidence of mechanisms that may facilitate some observed population-level differences in the degree of specialisation (e.g. in aphid host specificity, Bernays & Funk, 1999). A prediction related to the niche variation hypothesis is that specialist species (e.g. limited to utilising a single resource class) should be characterised by low levels of among-individual variation especially when they face inter-specific competition from ecologically similar species (Araújo *et al.*, 2011). Burying beetles (Nicrophorinae) ought to fall into this category, occupying a specialist niche and being subject to intense competition from conspecifics and often congeneric species (Trumbo, 1990a; Scott, 1998). However, burying beetles are noted for high levels of behavioural plasticity (e.g., Carter *et al.*, 2015; Creighton *et al.*, 2015), and exhibit striking body size variation within populations (Müller *et al.*, 2007; Hopwood *et al.*, 2014).

Burying beetles use small vertebrate carcasses as resources for feeding and reproduction, and having located a carcass they rear a discrete brood whose size is limited by the mass of the carcass (Eggert & Müller, 1997; Scott, 1998). Because broods are subject to a size-number trade off on each discrete carcass, offspring size is facultatively adjusted in burying beetles by parents tailoring brood size: females vary egg number laid, and both parents cannibalise first instar offspring according to carcass size (Bartlett, 1987; Smiseth & Moore, 2002; Creighton, 2005). Although offspring might often have the potential to grow larger, parents are primarily in control of the regulation of this trade-off and the direct and indirect payoffs that result. The potential conflict between parent and offspring over different body size optima are beyond the scope of this paper; here, we consider body size from the adult perspective. Intra-sexual contests over possession of carcass breeding resources are common, and even a small positive body size advantage usually predicts the victor (Hopwood *et al.*, 2013, 2014; Lee *et al.*, 2013). Differences in body size among species together with correlations between body size and carcass size preferences in species sharing the same range points to competitive exclusion delimiting community assembly (Pukowski, 1933; Scott, 1998). Body size differences among burying beetle species might, therefore, primarily be explained in terms of trait means, given that smaller beetle species are excluded from valuable large carcasses by larger species (Scott, 1998). However, this does not explain the high population-level body size variance.

One hypothesis is that individuals gain context-dependent benefits from utilising carcasses of a size appropriate to their own capabilities. For example, with a correlation between fecundity and maternal body size, large females will require a larger carcass than small females to rear their maximal brood (see Eggert & Müller, 1997; Steiger, 2013). This means a small carcass has a lower potential marginal value to a large beetle than to a small beetle. Furthermore, larger females, owing to the competitive benefits of their large size, are more likely to be able to force reproductive skew in their favour against competitors they encounter in the future (see Eggert & Müller, 2000, 2011; Eggert *et al.*, 2008). These factors mean that (depending on the frequency of suitable alternative carcasses in the wild) larger beetles might benefit by avoiding the costs of a low value reproductive attempt and searching for carcasses of a sufficient size to optimise lifetime reproductive output whereas smaller female beetles are expected to have a reduced imperative to risk the uncertainty of a resource 'upgrade'.

We, therefore, had specific predictions that we tested by manipulating the relationship between breeding resource (carcass) size and body size of the burying beetle *Nicrophorus vespilloides* (Herbst 1783) in the field and the laboratory. If benefits conferred by body size depend on resource size, we predicted assortative carcass use with beetle body size matching carcass size in the wild. This would support the niche variation hypothesis. Alternatively, a large body size might confer a general benefit because resource scarcity leads to a reproductive imperative to secure any and all breeding opportunities. In this case, we predicted that large beetles in the wild should not discriminate in their use of any viable carcass size. In the laboratory, we predicted large beetles would be more productive than small beetles on large carcasses. If indirect fitness benefits via producing large competitive offspring offset direct benefits of producing more offspring, we would predict that parents should tailor brood size towards achieving a single optimum offspring size regardless of their own size or the carcass size.

In the field, we placed pairs of wild-caught beetles in two size categories (large or small) on mouse carcasses that were either large or small and recorded breeding success or failure, and the number, species, and sex of wild competitors that arrived to contest each carcass. In the laboratory, we measured the reproductive output of pairs of wild-caught beetles in the same treatment categories as the wild experiment. This allowed us to measure differences in potential reproductive value related to differences between resource sizes.

Materials and methods

We captured beetles using funnel-type bottle traps baited with putrescent salmon during the summer of 2011 between late July and September to minimise the difference in age because early season captures would include post-diapause adults. Beetles were trapped in a mixed deciduous woodland in Cornwall, U.K. (coord: 50°11′60″N, 5°07′05″W) for use in experiment 1 (field). The same methods were used to obtain stock from the same woodland in 2012 for experiment 2 (laboratory). The capture site is approximately 1 km from the experimental site (coord: 50°11′42″N, 5°07′51″W), and the two sites are
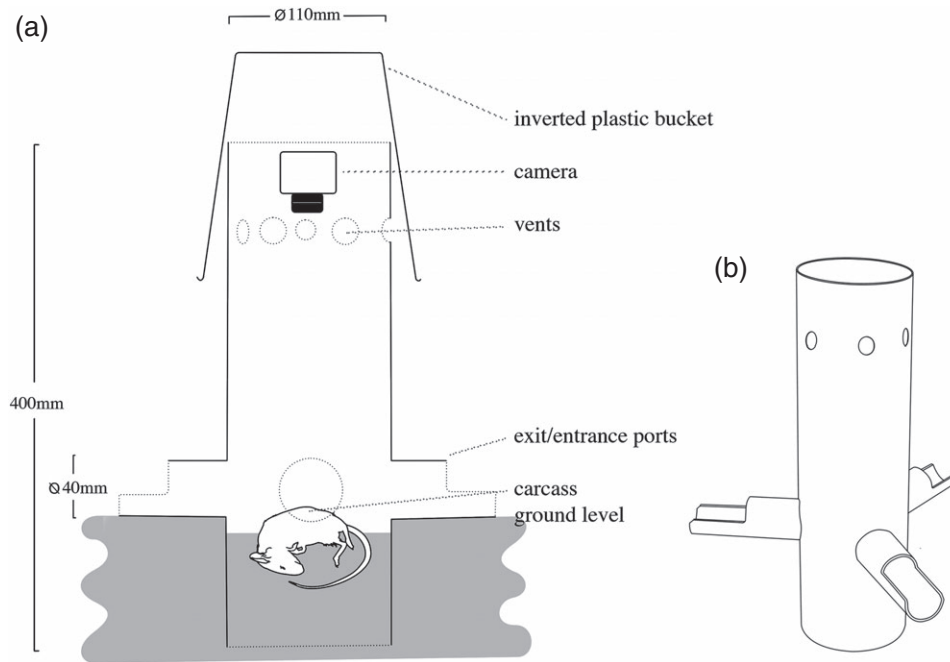
Fig. 1. Diagram of 'Nicrocosm' used to video beetle behaviour in the wild: (a) cutaway side-view with labels indicating dimensions and features; (b) oblique view showing Nicrocosm without inverted bucket for weather protection.

separated by a main road with open grass verges. Newly captured beetles were cleared of phoretic mites in the field (by blowing the mites off beetles using a sharp exhalation of breath directed through pursed lips). To ensure beetles were sexually mature and to reduce individual variation in nutritional status before their use in experiments, all captured beetles were housed individually in the laboratory as described in previous experiments (Hopwood *et al.*, 2013) and fed with two decapitated mealworms, *Tenebrio molitor* Linnaeus, twice per week. Laboratory beetles in experiment 2 were all used on day 8 after capture; beetles used for experiment 1 were used between 7 and 13 days after capture owing to logistical constraints in the field. There was no statistically significant difference between the treatment groups in the length of time pairs in experiment 1 were retained in the laboratory (ANOVA: $F_{3,60} = 0.400$, $P = 0.753$).

Experiment 1 (field)

Captured wild beetles were assigned to one of two size categories according to the distribution of pronotal width of the population. Beetles with pronota smaller or equal to 4.4 mm were randomly allocated a different-sex partner within their same size category (i.e. male and female) to produce 'small' pairs, whereas beetles with pronota greater than or equal to 5.0 mm were partnered with another beetle of the opposite sex by the same process. The size category limits were chosen to provide a reasonable number of individuals from both ends of the current size distribution of wild individuals and corresponded to the mean ± 1 SD of a contemporaneous wild-caught sample of beetles ($n = 235$).

The mean sizes of experimental beetles were: large female beetles = 5.29 ± 0.19 mm (mean ± SD); small female beetles = 4.10 ± 0.18 mm; large male beetles = 5.48 ± 0.20 mm; and small male beetles = 4.16 ± 0.25 mm. Individuals assigned to pairs were kept singly (i.e. for between 7 and 13 days) until used in the experiment. All beetles were marked with a small dot of white office correction fluid applied to a small (<1 mm²) area gently keyed with fine sandpaper on either the scutellum or pronotum (the position of the mark with respect to sex was randomised among pairs).

During the summer of 2011, 77 'Nicrocosms' (experimental arenas made of black plastic tubing enabling video capture of beetle behaviour in the field, Fig. 1 and see supplementary information in Hopwood *et al.*, 2013) in total were distributed, no more than six at any one time, in 0.4 ha of the experimental woodland with approximately 30 m between each. Either a large or a small (thawed, pre-frozen) mouse carcass was placed inside each on the natural soil substrate (each Nicrocosm was anchored in a hole to a depth of approximately 100 mm and the excavated soil was replaced inside to within 5 mm of ground level, see Fig. 1). Small mice were 5.48 ± 0.28 g (mean ± SD); large mice were 20.53 ± 0.31 g. This size range is represented in nature by mature shrews, small immature mammals, and songbird nestlings (~5 g) through to adult small mammals and small passerines (~20 g). It corresponds with other published studies on *N. vespilloides* that have used carcasses between 2 g to above 35 g (e.g., Otronen, 1988; Müller *et al.*, 1990; Smiseth & Moore, 2002; Steiger, 2013).

One pair of small or large beetles was introduced to each Nicrocosm (at approximately midday), containing a large or small carcass, before the natural late afternoon/early evening

activity period of this beetle species. The experimental groups, therefore, consisted of a pair of small beetles with either a large or a small carcass or a pair of large beetles with either a large or a small carcass.

Sixty-four Nicrocosms were included, using the criterion that both beetles in the pair made exploratory contact with the carcass. A motion-sensitive infrared camera with infrared light emitting diodes in each Nicrocosm (Fig. 1 and see supplementary information in Hopwood *et al.* (2013) for technical details) facilitated video data collection of information on number, species and sex of intruders, brood desertion and brood parasitic or satellite beetle behaviour. Any prenatal usurpation of the carcass was recorded and was defined as a challenge by a wild arriving conspecific or interspecific beetle(s) that successfully displaced a focal beetle from its dominant status on the carcass. Each reproductive event was terminated 5 days after carcass burial (or when larvae were first seen) and the carcass and resident beetles were disinterred to determine success in producing a clutch of eggs/larvae, to check whether the experimental female was on the carcass (see Scott & Traniello, 1990) and to confirm the number and sex of other adult beetles. These beetles were subsequently removed from the field site for the duration of the experiment to minimise any possible confounding artifact of their remaining and visiting other experimental carcasses nearby. Empty and exhumed Nicrocosms were cleaned and moved to a different location before fresh experimental occupants were introduced along with a fresh carcass (on the following day or as soon after that as prepared experimental animals were available).

Experiment 2 (laboratory)

In the summer of 2012, wild-caught beetles were prepared and assigned to pairs as for the experiment described above. Two large females laid no eggs on one small and one large carcass, respectively, and one small female laid infertile eggs on a large carcass. These three trials were re-established with fresh viable pairs (i.e. making: $n = 20$ pairs in each group, total: $n = 80$). The factorial groups were the same as for experiment 1 and the experimental design was similar except that beetle pairs bred under controlled conditions in the laboratory. Large female beetles were 5.32 ± 0.26 mm (mean $\pm$ SD); small female beetles were 3.97 ± 0.17 mm. Large male beetles were 5.45 ± 0.24 mm; small male beetles were 4.08 ± 0.23 mm. Each experimental pair was provided with a mouse carcass [small $= 5.54 \pm 0.28$ g (mean $\pm$ SD); large $= 20.54 \pm 0.31$ g] in a plastic breeding box ($17 \times 11 \times 5$ cm^3) with approximately 3-cm-moist compost to enable natural reproductive behaviour. Beetles were undisturbed for the duration of each reproductive bout and larvae produced were weighed and measured at dispersal i.e. when fully developed with at least two larvae witnessed wandering from the depleted carcass remains (Rauter & Moore, 2002).

Statistical analyses

Rejection of breeding resources was defined as a beetle making exploratory contact with the carcass (see Hopwood

et al., 2015) but then leaving, in the absence of any direct competitor(s), within 4 days, and with no evidence of eggs or larvae on carcass disinterment. Because male success depends upon female utilisation of the carcass, our analyses focus on the female of the pair (the same qualitative result was obtained when rejection by the male individual, or both beetles in the pair, was analysed; results not shown). We analysed carcass rejection using Fisher's exact tests applied to the number of females in each body size category that deserted their carcass without breeding. Usurpation of the breeding resource was defined as the female of the focal pair being displaced by a wild beetle before any larvae appeared (yes or no) and analysed using a generalised linear model with binomial errors with beetle size and carcass size as fixed categorical factors. In the laboratory experiment, brood mass and individual offspring size were both analysed using linear models. Both models included carcass size (large or small) and parental pair size (large or small) as categorical fixed factors. All analyses were performed using 'R' version 2.14.1 (R Development Core Team, 2011) with multivariate linear models simplified using a stepwise approach (Crawley, 2007). Means are presented ± 1 standard error unless stated otherwise.

Results

Experiment 1 (field)

Large female beetles rejected more small carcasses than they did large carcasses (Fisher's exact test: $n = 32$, $P = 0.023$, Table 1a) but small beetles did not differ in the number of small or large carcasses rejected (Fisher's exact test: $n = 32$, $P = 1$, Table 1b). The incidence of usurpation by intruders was low, and no wild beetles arrived after the carcass was buried in this study. Although 14 out of 64 carcasses were visited by conspecific female intruders, in only four instances was the female displaced forcibly by a rival who then used the carcass to breed successfully (one large female from a large carcass; two small females from large carcasses and one small female from a small carcass). One further female (small, on a small carcass) was replaced by an intruding female that did not subsequently breed successfully. Two focal males were displaced: one large male from a large carcass and one small male from a small carcass were also usurped. As a consequence of this low power, neither female size ($\chi^2_1 = 2.080$, $P = 0.149$), carcass size ($\chi^2_1 = 0.225$, $P = 0.635$) nor the interaction between them ($\chi^2_1 = 1.193$, $P = 0.275$) predicted usurpation of the breeding resource.

Experiment 2 (laboratory)

Reproductive output was affected by an interaction between parental size and carcass size: large beetles reared heavier broods than small beetles on large carcasses (total brood mass), but small beetles reared heavier broods on small carcasses (LM, parental size $\times$ carcass size: $F_{1,76} = 19.528$, $P < 0.0001$, Fig. 2a). The main effects of carcass size ($F_{1,77} = 352.11$, $P < 0.0001$) and parental size ($F_{1,77} = 4.881$, $P = 0.030$) were also significant. The average offspring mass differed between carcasses: the

Table 1. The number of focal female beetles that (in the absence of competitors) used their carcass for breeding or rejected carcass without laying eggs. (a) The number of carcasses used and rejected by large females ($n = 32$); (b) number of carcasses used and rejected by small females ($n = 32$).

	(a) Large beetles		(b) Small beetles	
Carcass size	Focal female rejects carcass	Focal female uses carcass	Focal female rejects carcass	Focal female uses carcass
Large carcass	2	14	3	13
Small carcass	9	7	3	13

small offspring were produced on small carcasses and large carcasses on large carcasses (carcass size: LM, $F_{1,78} = 69.928$, $P < 0.0001$, Fig. 2b). Controlling for carcass size, there was no significant difference in mass between offspring reared by large or small parents (parental size: $F_{1,77} = 0.108$, $P = 0.744$) and the interaction between parent size and offspring size also was not significant ($F_{1,76} = 0.960$, $P = 0.330$).

Discussion

Evidence from our field experiment supports individual specialisation in resource use in *N. vespilloides*. Large female beetles were significantly more likely to reject small carcasses than large carcasses, but small female beetles did not differentiate between carcasses of the two size categories (Table 1). This pattern is not fully explained by intrinsic incompatibility owing to a large body size (e.g. large beetles might require too large a proportion of carrion from a small carcass for their own nutrition, rendering successful breeding impossible) because in controlled laboratory conditions when confined to a carcass, similarly matched large beetle pairs successfully raised broods on carcasses of a similar size as those provided in the field (Fig. 2). The selective mechanism underlying the differential motivation to utilise carcasses between large and small female beetles is unknown but differences in potential residual reproductive value related to carcass size may provide a target on which selection can act (see also Ward *et al.*, 2009). Previously published studies on *N. vespilloides* and *N. orbicollis* have looked for, but found no evidence, that adult body size has a significant effect on longevity that might have suggested a terminal investment interpretation of our field results (Bartlett & Ashworth, 1988; Ward, 2008; Trumbo & Rauter, 2014 and see Trumbo, 2009). In the laboratory, reproductive output was affected by an interaction between parental body size and carcass size. Because large beetles outperformed small beetles when breeding on large carcasses, the difference in marginal reproductive value between carcasses of a different size is wider for large female beetles than for small females (and perhaps for males of any size). We are cautious in the interpretation of the statistically significant difference in brood mass between large beetles and small beetles when they bred on small carcasses because the difference may be too small to have adaptive, biological significance. Moreover, it is possible
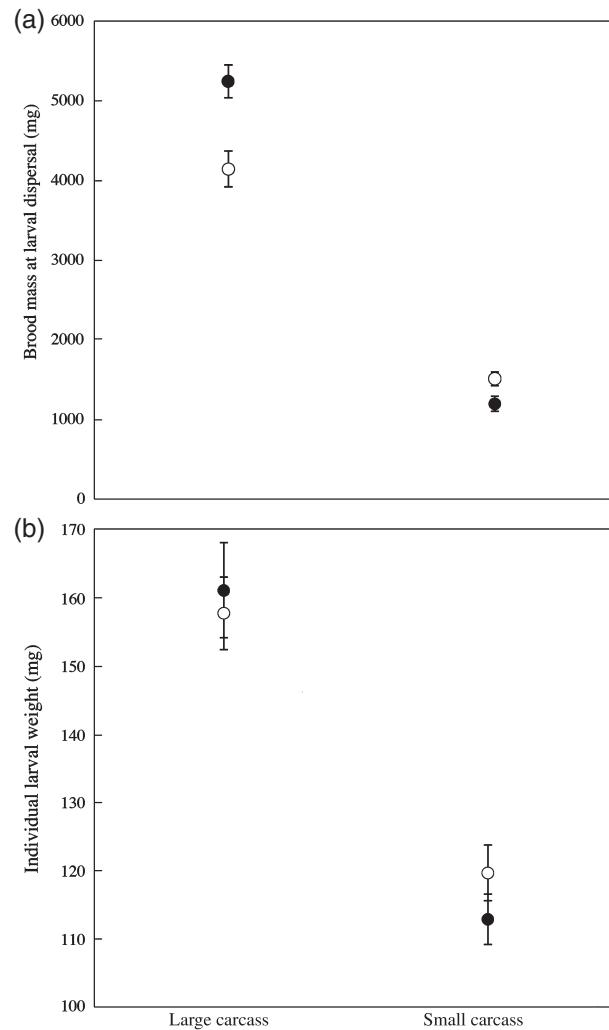

Fig. 2. (a) Large beetles rear a larger brood than small beetles on large carcasses, but small beetles rear a larger brood than large beetles on small carcasses. (b) Offspring size is determined by carcass size, independent of parental size, i.e. offspring from large carcasses are large whereas those from small carcasses are small. Solid circles = large parents; open circles = small parents. Means ± 1 standard error displayed.

that on small carcasses there is a differential male effect if large males impact broods more than small males (e.g. by feeding on the carcass themselves or cannibalism of larvae) when their natural male early desertion is artificially delayed in the laboratory.

There is considerable evidence that even a slight relative size advantage predicts success in intraspecific contests in burying beetles (Bartlett & Ashworth, 1988; Otronen, 1988; Hopwood *et al.*, 2013, 2014; Lee *et al.*, 2013) and large size is likely to aid successful resource defence against interspecific beetle competitors (Robertson, 1993; Trumbo, 2006, 2007). However, an overall disadvantage (and the extent of any disadvantage) for small individuals depends upon the frequency of such competitive encounters in an ecological context and the impact on individual reproductive success. Here we found that less than 24% of carcasses (i.e. 14 out of 64 carcasses) attracted

intruding female rivals and of those that did only 4 intruders successfully usurped the current resource holding female beetle in a successful breeding event (out of 54 carcasses that produced larvae). No carcasses were lost to inter-specific burying beetle competitors. We used pairs rather than single females to provide beetles with an immediate opportunity to breed but in nature, if a male arrived at an unoccupied carcass the delay involved while he calls (i.e. releases pheromones) for a female might increase the risk of carcass discovery by rivals. Furthermore, rival males or additional females may arrive in response to a calling male (Müller & Eggert, 1987). In the field experiment, once a pair of beetles had possession of a carcass (i.e. it was not rejected) they were more likely than not to retain it. Usurpation by competitors always occurred prior to the arrival of larvae, and we witnessed neither reversals of contest outcomes nor successful carcass takeovers by intruders after larvae arrived. The low incidence of usurpation we observed thus limits our ability to quantify the effect body size might have on securing breeding opportunities in nature but nonetheless evidence from both experiments suggests that a body size-mediated contest advantage is not the only factor determining a successful breeding attempt after a carcass is located.

Body size, resource variation, and community structure

Character displacement along several axes including the mean body size, daily activity period, and the seasonal activity period appears to permit interspecific coexistence in these beetles (Pukowski, 1933; Scott, 1998; Kočárek, 2001). This pattern is described in many locations often with different constituent species (e.g. Müller & Eggert, 1987; Scott & Traniello, 1987; Otronen, 1988; Trumbo, 1994; Suzuki, 2000; Kočárek, 2001). In our study population *N. vespilloides* is the smallest of five burying beetles (N. *humator*, N. *investigator*, N. *interruptus*, N. *vespillo*, and N. *vespilloides* in descending order of the mean body size) and competition with interspecifics for very small carcasses may, therefore, be relaxed. Individual specialisation may affect the distribution of correlated morphological traits among populations. Our results suggest that within-population phenotypic variance in *N. vespilloides* may primarily reflect size variation in available carcasses (see also: Bartlett & Ashworth, 1988; Eggert & Müller, 1997; Hopwood *et al.*, 2014, and in the similarly small *N. defodiens*: Scott & Traniello, 1990) and this environmental source of trait variation may alter the dynamics of interspecific community assembly (Meyers & Bull, 2002; Bolnick *et al.*, 2003; Violle *et al.*, 2012). This is because trait mean and variance of beetle body size will likely vary among populations experiencing different local communities of vertebrates.

Mechanisms of selection on body size

In the laboratory, we found an apparent trade-off directly involving reproductive potential and body size because large beetles reared > 20% more offspring on large carcasses than did small beetles but were outperformed themselves by small beetles on small carcasses. One explanation is that small females were simply unable to produce eggs in sufficient numbers and/or in time to populate large carcasses (Steiger *et al.*, 2007; Steiger, 2013). However, there is a puzzle because small beetles having produced fewer offspring on a larger carcass nevertheless reared individuals of a similar size as did large beetles. The expectation would be for larger offspring to be produced when fewer compete for the same finite resource. We do not believe this was an artifact of confining males of different sizes to the breeding boxes beyond their natural desertion time (when excessive artificial delays could result in occasional late cannibalism of larvae) because even if this occurred we would still expect the fewer larvae from small parents on large carcasses to grow larger than broods on large carcasses from large parents (Steiger *et al.*, 2007). One likely explanation is that small beetle parents are unable to prepare, process, and maintain large carcasses as efficiently as can large parents. If this is true, the fewer larvae that small females produce might struggle to utilise the whole potential of a large carcass, and more of the carcass will remain unused by the brood. In this experiment, we did not weigh carcass remains after larval development. The same pattern but reversed (i.e. offspring mean mass reflected carcass mass, not offspring number or parental body size) was also observed on small carcasses suggesting that costs of the provision of parental care related to size were unlikely to account for the effect (see also Hopwood *et al.*, 2014). In our study, larvae did not achieve their physiological maximum body size in either carcass treatment as larvae of this species grow to over 200 mg when the relationship between brood size and carcass size is manipulated experimentally, even on intermediate carcass sizes (e.g. Lock *et al.*, 2007).

In burying beetles, parental provisioning and carcass maintenance can have a significant influence on offspring growth and development (Rauter & Moore, 2002; Head *et al.*, 2012). However, an important additional metric of parental care performance is actively tailoring offspring number to carcass size through regulating prenatal oviposition (number of eggs laid) and postnatal filial cannibalism (Bartlett, 1987; Trumbo, 1990b; Eggert & Müller, 1997; Scott, 1998). This parental brood tailoring is sufficiently accurate in some species to produce similar sized offspring across a range of carcass sizes although studies that found this used carcasses within a more limited range than the four-fold difference in our experiment (e.g. Wilson & Fudge, 1984; Trumbo, 1990b; Trumbo & Fernandez, 1995). Thus, variation in maternal control (or physiological limitation) of oviposition and parental infanticidal behaviour can have profound and immediate effects on offspring performance. It is still not clear how selection shapes parental brood tailoring rules-of-thumb (see: Creighton, 2005; Steiger *et al.*, 2007; Rauter *et al.*, 2010) but there is evidence in *N. vespilloides* that the behaviours are plastic and affected by maternal nutritional condition, and in *N. defodiens* that it has a genetic basis (Steiger *et al.*, 2007). Carcass volume appears to be the cue indicating resource size by which burying beetles make brood size decisions (Trumbo & Fernandez, 1995) and perhaps this also indicates a threshold resource value related to maternal size. We found that parental brood tailoring does not produce similar-sized offspring across carcasses that have a wide difference in size. Although this finding is not clear evidence that there is no single

optimal body size for *N. vespilloides*, the possibility exists that there are body size-dependent ecological or strategic differences that may offset the apparent disadvantage of being a small burying beetle.

Fox and Mousseau (1998) hypothesised that a transgenerational non-genetic phenotypic correlation could be maintained in a randomly mating population if female early host experience (e.g. in a herbivorous insect) influenced both oviposition preference and offspring performance. This is distinct from an indirect genetic effect that relies on the genetic heritability of a parental phenotype that influences an offspring phenotype. Our results supporting individual variation in resource use, combined with the effect of carcass size on offspring size, suggest another mechanism of 'soft' inheritance of body size (Bonduriansky, 2012). In our laboratory experiment (and see Hopwood *et al.*, 2014), we found that offspring body size reflected differences in carcass size independent of parental size variation (Fig. 2b). Assortative carcass use observed in the field could facilitate a non-genetic mechanism of phenotypic inheritance producing transgenerational patterns of differences in size and behaviour. By rejecting small carcasses in favour of large for breeding, large mothers are 'reconstructing' the developmental environment that influenced their own body size (Uller, 2012; Uller & Helanterá, 2013).

Conclusions

We found evidence supporting individual niche variation mediated by body size: a significant proportion of large beetles (but not small) rejected small potential breeding resources in the field. In laboratory conditions where opportunities for deserting were restricted, this did not occur and pairs of beetles reproduced successfully regardless of their size or the size of the carcass. However, maximum reproductive output depended on an optimal match between resource size and parental body size and although large beetles outperformed small beetles when breeding on large carcasses, small beetles were more successful than were large beetles when they bred on small carcasses. Individual preference for breeding resource use depended on a relationship between resource size and body size, and body size itself is determined by the carcass size on which the individual was reared. These findings demonstrate a process by which phenotypic variance is actively maintained via an environmental feedback and suggest a non-genetic mechanism by which transgenerational inheritance of body size might occur in this species.

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References

Ackermann, M. & Doebeli, M. (2004) Evolution of niche width and adaptive diversification. *Evolution*, **58**, 2599–2612.

Andersson, M.B. (1994) *Sexual Selection*. Princeton University Press, Princeton, New Jersey.

Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011) The ecological causes of individual specialisation. *Ecology Letters*, **14**, 948–958.

Bartlett, J. (1987) Filial cannibalism in burying beetles. *Behavioral Ecology and Sociobiology*, **21**, 179–183.

Bartlett, J. & Ashworth, C.M. (1988) Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behavioral Ecology and Sociobiology*, **22**, 429–434.

Bernays, E.A. & Funk, D.J. (1999) Specialists make faster decisions than generalists: experiments with aphids. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 151–156.

Blanckenhorn, W.U. (2005) Behavioral causes and consequences of sexual size dimorphism. *Ethology*, **111**, 977–1016.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. *et al.* (2003) The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, **161**, 1–28.

Bolnick, D.I., Svanbäck, R., Araújo, M.S. & Persson, L. (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 10075–10079.

Bonduriansky, R. (2012) Rethinking heredity, again. *Trends in Ecology & Evolution*, **27**, 330–336.

Carter, M.J., Head, M.L., Moore, A.J. & Royle, N.J. (2015) Behavioral plasticity and G×E of reproductive tactics in *Nicrophorus vespilloides* burying beetles. *Evolution*, **69**, 969–978.

Crawley, M.J. (2007) *The R Book*. John Wiley and Sons, Chichester, U.K.

Creighton, J.C. (2005) Population density, body size, and phenotypic plasticity of brood size in a burying beetle. *Behavioural Ecology*, **16**, 1031–1036.

Creighton, J.C., Smith, A.N., Komendat, A. & Belk, M.C. (2015) Dynamics of biparental care in a burying beetle: experimental handicapping results in partner compensation. *Behavioral Ecology and Sociobiology*, **69**, 265–271.

Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex*. John Murray, London, U.K.

Eggert, A.K. & Müller, J.K. (1997) Biparental care and social evolution in burying beetles: lessons from the larder. *The Evolution of Social Behavior in Insects and Arachnids* (ed. by J. C. Choe and B. J. Crespi), pp. 216–236. Princeton University Press, Princeton, New Jersey.

Eggert, A.K. & Müller, J.K. (2000) Timing of oviposition and reproductive skew in cobreeding female burying beetles (Nicrophorus vespilloides). *Behavioral Ecology*, **11**, 357–366.

Eggert, A.K. & Müller, J.K. (2011) Timing of oviposition enables dominant female burying beetles to destroy brood-parasitic young. *Animal Behaviour*, **82**, 1127–1233.

Eggert, A.K., Otte, T. & Müller, J.K. (2008) Starving the competition: a proximate cause of reproductive skew in burying beetles (*Nicrophorus vespilloides*). *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2521–2528.

Fox, C.W. & Mousseau, T.A. (1998) Maternal effects as adaptations for transgenerational phenotypic plasticity in insects. *Maternal Effects as Adaptations* (ed. by T. A. Mousseau and C. W. Fox), pp. 159–177. Oxford University Press, Oxford, U.K.

Head, M.L., Berry, L.K., Royle, N.J. & Moore, A.J. (2012) Paternal care: direct and indirect genetic effects of fathers on offspring performance. *Evolution*, **66**, 3570–3581.

Hopwood, P.E., Moore, A.J. & Royle, N.J. (2013) Nutrition during sexual maturation affects competitive ability but not reproductive productivity in burying beetles. *Functional Ecology*, **27**, 1350–1357.

Hopwood, P.E., Moore, A.J. & Royle, N.J. (2014) Effects of resource variation during early life and adult social environment on contest outcomes in burying beetles: silver spoon or context-dependent strategy? *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133102.

Hopwood, P.E., Moore, A.J., Tregenza, T. & Royle, N.J. (2015) Male burying beetles extend, not reduce, parental care duration when reproductive competition is high. *Journal of Evolutionary Biology*, **28**, 1394–1402.

Kočárek, P. (2001) Diurnal activity rhythms and niche differentiation in a carrion beetle assemblage (Coleoptera: Silphidae) in Opava, the Czech Republic. *Biological Rhythm Research*, **32**, 431–438.

Lee, V.E., Head, M.L., Carter, M.J. & Royle, N.J. (2013) Effects of age and experience on contest behaviour in the burying beetle, *Nicrophorus vespilloides*. *Behavioural Ecology*, **25**, 172–179.

Lock, J.E., Smiseth, P.T., Moore, P.J. & Moore, A.J. (2007) Coadaptation of prenatal and postnatal maternal effects. *American Naturalist*, **170**, 709–718.

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, **101**, 377–385.

Meyers, L.A. & Bull, J.J. (2002) Fighting change with change: adaptive variation in an uncertain world. *Trends in Ecology & Evolution*, **17**, 551–557.

Morse, D.H. (1974) Niche breadth as a function of social dominance. *American Naturalist*, **108**, 818–830.

Müller, J.K. & Eggert, A.K. (1987) Effects of carrion-independent pheromone emission by male burying beetles (Silphidae: *Nicrophorus*). *Ethology*, **76**, 297–304.

Müller, J.K., Eggert, A.K. & Furlkröger, E. (1990) Clutch size regulation in the burying beetle *Nicrophorus vespilloides* Herbst (Coleoptera: Silphidae). *Journal of Insect Behavior*, **3**, 265–270.

Müller, J.K., Braunisch, V., Hwang, W. & Eggert, A.K. (2007) Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*. *Behavioural Ecology*, **18**, 196–203.

Otronen, M. (1988) The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Annales Zoologici Fennici*, **25**, 191–201.

Price, T.D. (1987) Diet variation in a population of Darwin's finches. *Ecology*, **68**, 1015–1028.

Pukowski, E. (1933) Ökologische untersuchungen an Necrophorus F. *Zoomorphology*, **27**, 518–586.

Rauter, C.M. & Moore, A.J. (2002) Evolutionary importance of parental care performance, food resources, and direct and indirect genetic effects in a burying beetle. *Journal of Evolutionary Biology*, **15**, 407–417.

Rauter, C.M., Mcguire, M.J., Gwartney, M.M. & Space, J.E. (2010) Effect of population density and female body size on number and size of offspring in a species with size-dependent contests over resources. *Ethology*, **116**, 120–128.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria [WWW document]. URL http://www.R-project.org [accessed on 4 October 2011].

Robertson, I.C. (1993) Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera: Silphidae). *Journal of Zoology*, **231**, 583–593.

Roff, D.A. (2002) *Life History Evolution*. Sinauer Associates Inc., Massachusetts, Sunderland.

Roughgarden, J. (1974) Niche width: biogeographic patterns among Anolis lizard populations. *American Naturalist*, **108**, 429–442.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

Scott, M.P. (1998) The ecology and behavior of burying beetles. *Annual Review of Entomology*, **43**, 595–618.

Scott, M.P. & Traniello, J.F.A. (1987) Behavioural cues trigger ovarian development in the burying beetle, *Nicrophorus tomentosus*. *Journal of Insect Physiology*, **33**, 693–696.

Scott, M.P. & Traniello, J.F.A. (1990) Behavioural and ecological correlates of male and female parental care and reproductive success in burying beetles (*Necrophorus* spp.). *Animal Behavior*, **39**, 274–283.

Shine, R. (1988) The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. *American Naturalist*, **131**, 124–131.

Smiseth, P.T. & Moore, A.J. (2002) Does resource availability affect offspring begging and parental provisioning in a partially begging species? *Animal Behaviour*, **63**, 577–585.

Steiger, S. (2013) Bigger mothers are better mothers: disentangling size-related prenatal and postnatal maternal effects. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131225.

Steiger, S., Richter, K., Müller, J.K. & Eggert, A.K. (2007) Maternal nutritional condition and genetic differentiation affect brood size and offspring body size in Nicrophorus. *Zoology*, **110**, 360–368.

Suzuki, S. (2000) Changing dominant-subordinate relationships during carcass preparation between burying beetle species (Nicrophorus: Silphidae: Coleoptera). *Journal of Ethology*, **18**, 25–28.

Trumbo, S.T. (1990a) Interference competition among burying beetles (Silphidae, Nicrophorus). *Ecological Entomology*, **15**, 347–355.

Trumbo, S.T. (1990b) Regulation of brood size in a burying beetle, Nicrophorus tomentosus (Silphidae). *Journal of Insect Behavior*, **3**, 491–500.

Trumbo, S.T. (1994) Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. *Oikos*, **69**, 241–249.

Trumbo, S.T. (2006) Infanticide, sexual selection and task specialization in a biparental burying beetle. *Animal Behaviour*, **72**, 1159–1167.

Trumbo, S.T. (2007) Defending young biparentally: female risk-taking with and without a male in the burying beetle, *Nicrophorus pustulatus*. *Behavioral Ecology and Sociobiology*, **61**, 1717–1723.

Trumbo, S.T. (2009) Age-related reproductive performance in the parental burying beetle, Nicrophorus orbicollis. *Behavioral Ecology*, **20**, 951–956.

Trumbo, S.T. & Fernandez, A.G. (1995) Regulation of brood size by male parents and cues employed to assess resource size by burying beetles. *Ethology Ecology and Evolution*, **7**, 313–322.

Trumbo, S.T. & Rauter, C.M. (2014) Juvenile hormone, metabolic rate, body mass and longevity costs in parenting burying beetles. *Animal Behaviour*, **92**, 203–211.

Uller, T. (2012) Parental effects in development and evolution. *The Evolution of Parental Care* (ed. by N. J. Royle, P. T. Smiseth and M. Kölliker), pp. 247–266. Oxford University Press, Oxford, U.K.

Uller, T. & Helanterá, H. (2013) Non-genetic inheritance in evolutionary theory: a primer. *Non-Genetic Inheritance*, **1**, 27–32.

Van Valen, L. (1965) Morphological variation and width of ecological niche. *American Naturalist*, **99**, 377–390.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C. *et al.* (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, **27**, 244–252.

Ward, R.J.S. (2008) *Ageing and reproductive strategies in the burying beetle Nicrophorus vespilloides*. PhD thesis, University of Cambridge, Cambridge, U.K.

Ward, R.J.S., Cotter, S.C. & Kilner, R.M. (2009) Current brood size and residual reproductive value predict offspring desertion in the burying beetle Nicrophorus vespilloides. *Behavioral Ecology*, **20**, 1274–1281.

Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, **15**, 393–425.

Wilson, D.S. & Fudge, J. (1984) Burying beetles: intraspecific interactions and reproductive success in the field. *Ecological Entomology*, **9**, 195–203.