

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

Running title: Niche variation in a specialist 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 interspecific resource competition, is that individuals might assort according to body size on different sized breeding-resources.

3. We tested the 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. Our 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; niche variation; individual specialisation; non-genetic inheritance.

Introduction:

Benefits of 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 interspecific niche partitioning (MacArthur and 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 and 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).

Intraspecific competition is one mechanism that might drive individual resource-use specialisation, for example, if subdominant or smaller individuals are relegated to alternative or inferior 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 and Doebeli 2004). A classic example is the medium ground finch, *Geospiza fortis*, 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 and Funk 1999). A prediction related to the niche variation hypothesis is that specialist species (e.g. limited to utilizing a single resource class) should be characterised by low levels of among-individual variation especially when they face interspecific 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 and 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 1st instar offspring according to carcass size (Bartlett, 1987; Smiseth and 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. Intrasexual 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; Lee et al. 2013; Hopwood et al. 2014). 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 high population-level body size variance. One hypothesis is that individuals gain context-dependent benefits from utilizing 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 lower potential marginal value to a large beetle than to a small beetle. Furthermore, larger females, due 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 sufficient size to optimise lifetime reproductive output while 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* in the field and in 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, 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, UK (coord: N50° 11' 60", W5° 07' 05") 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 1km from the experimental site (coord: N50° 11' 42", W5° 07' 51") and the two sites are 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*, twice per week. Laboratory beetles in experiment 2 were all used on day eight after capture; beetles used for experiment 1 were used between 7 and 13 days after capture due to logistical constraints in the field. There was no statistically significant difference among 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 4.4mm were randomly allocated a different-sex partner within their same size category (i.e., male and female) to produce ‘small’ pairs, while beetles with pronota greater than or equal to 5.0mm 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 \pm SD); small female beetles = 4.10 ± 0.18 mm; large male beetles = 5.48 ± 0.20 mm; 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 ($<1\text{mm}^2$) area gently keyed with fine sandpaper on either the scutellum or pronotum (the position of the mark with respect to sex was randomized 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 30m 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 100mm and the excavated soil was replaced inside to within 5mm of ground level, see Fig. 1). Small mice were 5.48 ± 0.28 g (mean \pm SD);

large mice were 20.53 ± 0.31 g. This size range is represented in nature by mature shrews, immature small mammals and songbird nestlings (~5g) through to adult small mammals and small passerines (~20g). It corresponds with other published studies on *N. vespilloides* that have used carcasses between 2g to above 35g (e.g., Otronen 1988; Müller et al. 1990; Smiseth and Moore 2002; Steiger 2013).

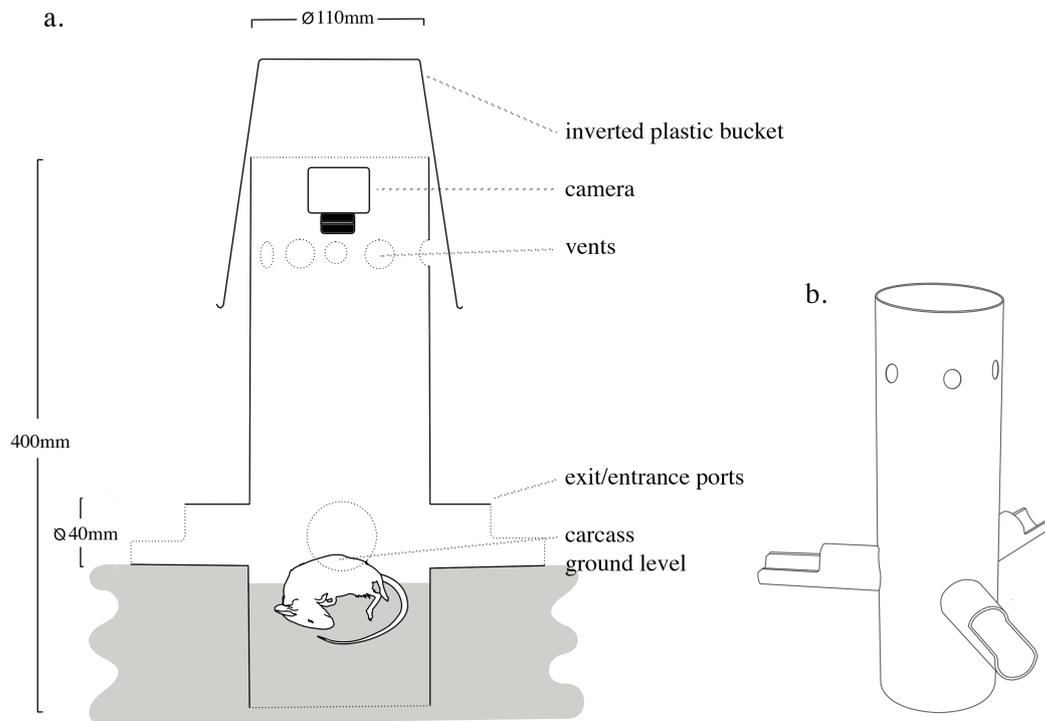


Figure 1: Diagram of ‘Nicrocosm’ used to video beetle behaviour in the wild: a) cutaway side-view with labels indicating dimensions and features; b) oblique view showing Nicrocosm without inverted bucket for weather protection.

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.

64 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.* (2014) 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 five 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 and 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 minimize 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 ± 0.28 g (mean \pm SD); large = 20.54 ± 0.31 g) in a plastic breeding box ($17 \times 11 \times 5$ cm) with about 3cm 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 and 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 four 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 categorical fixed 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 \pm 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.

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

Carcass size	a. large beetles		b. small beetles	
	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

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. Average offspring mass differed between carcasses: 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 ($F_{1,76} = 0.960$, $p = 0.330$).

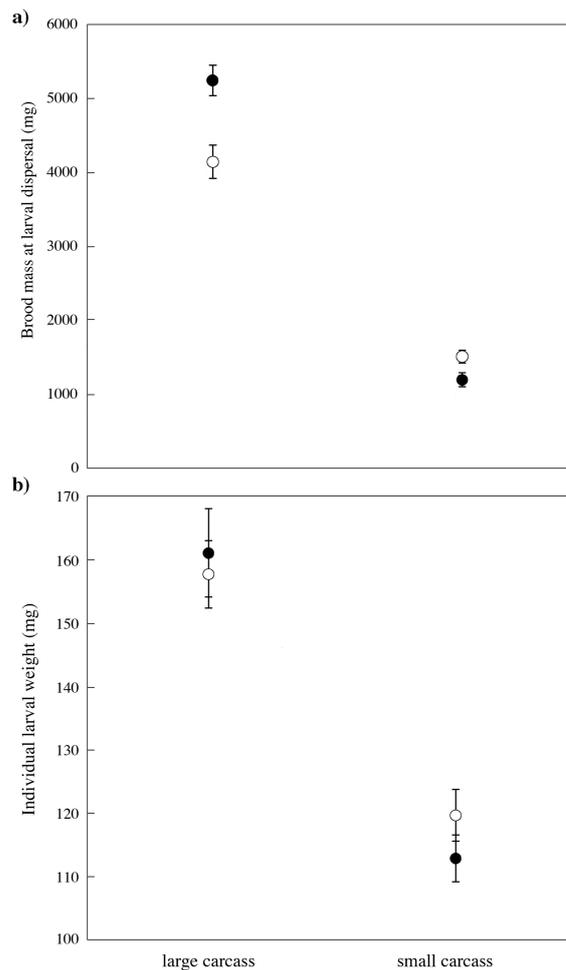


Figure 2: a) Large beetles rear a larger brood than small beetles on large carcasses, but small beetles rear a larger brood than large beetles on small carcasses. b) Offspring size is determined by carcass size, independent of parental size, i.e., offspring from large carcasses are large while those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

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 due to 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 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; Trumbo & Rauter, 2014; Ward, 2008 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 different size is wider for large female beetles than for small females (and perhaps for males of any size). We are cautious in 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 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 and Ashworth 1988;

Otronen 1988; Hopwood et al. 2013; Lee et al. 2013; Hopwood et al. 2014) 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 interspecific 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 and 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 mean body size, daily activity period and 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 and Eggert 1987; Scott and 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 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 and 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, 2013; Steiger et al., 2007). However, there is a puzzle because small beetles having

produced fewer offspring on a larger carcass nevertheless reared individuals of 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 don't 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 200mg 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 and 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 and Fudge 1984; Trumbo 1990b; Trumbo and 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; Rauter et al. 2010; Steiger et al. 2007) 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 and 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 size 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 & 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

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 and 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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Contribution of authors: PEH collected and analysed the data. All authors designed the experiments and co-wrote the manuscript. Data are available at University of Exeter: ORE repository.

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