Early-life effects on body size in each sex interact to determine reproductive success in the burying beetle *Nicrophorus vespilloides*

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Abstract

Early-life conditions have been shown to have a profound effect on an animal's body size and fecundity across diverse taxa. However, less is known about how early-life effects on fecundity within each sex interact to determine reproductive success. We used experiments with burying beetles *Nicrophorus vespilloides* to analyse this problem. The nutritional conditions experienced by burying beetles in early life are a key determinant of adult body size in both sexes, and adult body size in turn influences male reproductive tactics. In previous work, we showed that smaller males are more effective than larger males at stimulating virgin female fecundity. In this study, we manipulated male and female body size by restricting access to food in early development. We then conducted breeding assays, in which small and large females were mated sequentially with small and large males, and then allowed to raise offspring without paternal care. We tested whether large females, which are potentially more fecund, laid even more eggs when mated with small males. We found no evidence to support this prediction. Instead, we detected only a weak non-significant trend in the predicted direction and no equivalent trend in the number of larvae produced. However, we did find that larvae attained a greater mass by the end of development when their mother was large and mated with a small male first. We suggest that large females might have evolved counter-measures that prevent exploitation by small fecundity-stimulating males, including partial filial cannibalism. By eating surplus larvae during reproduction, larger females would leave more of the carrion for their offspring to consume. This could explain why their surviving larvae are able to attain a greater mass by the time they complete their development.

**KEYWORDS**

body size, early-life effects, fecundity stimulation, filial cannibalism, *Nicrophorus vespilloides*, nuptial gifts
INTRODUCTION

It is now well-established that environmental conditions experienced in early life have profound effects on traits expressed in later life (Lindström, 1999; Monaghan, 2008; Moore & Martin, 2019). The nutritional environment, social environment and thermal environment experienced during development can each independently influence an individual's physiology and behaviour in adulthood, and hence contribute to their fecundity (Barrett et al., 2009; Hopwood et al., 2016; Metcalfe & Monaghan, 2003; Monaghan & Metcalfe, 2019; Sedinger et al., 1995). Nevertheless, in sexually reproducing animals, it takes more than one phenotype to produce offspring. It is not clear whether early-life effects can be exacerbated or mitigated by the early-life conditions experienced by an individual's sexual partner (but see e.g. Kilner et al., 2015). Nor is it known how the early-life conditions of multiple mates might interact to affect reproductive success.

Early-life conditions are especially likely to affect subsequent reproductive success when they contribute to an individual's size and where an adult's size, in turn, influences its social dominance (Altmann & Alberts, 2005; Barrett et al., 2009; Dey et al., 2014; Hodge et al., 2008; Smith, 1986). Male reproductive success is strongly skewed in favour of the socially dominant, often larger, individuals in many animal species, and it commonly causes subordinate males to adopt alternative mating tactics to make the best of a bad job (Clutton-Brock, 2016; Emlen, 1997; Hardy & Briffa, 2013). Recent work has shown that alternative tactics are deployed after mating too, when males compete for paternity (Alonzò & Pizzi, 2010; Cameron et al., 2007; Parker & Pizzari, 2010; Pascoal et al., 2018; Perry et al., 2013). In burying beetles, for example, socially dominant (larger) males compete for paternity by mating last and outcompeting the sperm deposited by the female's previous mates. By contrast, socially subordinate (smaller) males mate first and stimulate females to lay additional eggs. Although their share of paternity is low, subordinate males can nevertheless increase the absolute number of offspring they sire by stimulating female fecundity (Pascoal et al., 2018).

Whether they are competing for mates, or competing for fertilizations, male reproductive success is also contingent on a female's capacity to produce and raise offspring. This too, is likely to vary with a female's size, and therefore will also depend on the conditions that she experienced during development (Griffith & Buchanan, 2010; Jobson et al., 2015; Moore & Martin, 2019; Vargas et al., 2012). Across taxa, larger females lay more eggs (Honék, 1993), produce better-nourished eggs (Brooks et al., 1997), and provide superior care for their young (Rollinson & Rowe, 2015; Steiger, 2013). In all these ways, they offer a more valuable prize when males compete for mates. Furthermore, through their greater fecundity, larger females might additionally be induced to produce disproportionately more offspring after mating with fecundity-stimulating males (Chapman & Davies, 2004; Fedorka & Mousseau, 2002; Perry et al., 2013). At the same time, larger females might be more capable of physically resisting unwanted mating attempts by males (Han & Jablonski, 2018) or exerting control via postcopulatory mechanisms when a male attempts to gain fitness at the female's expense (Firman et al., 2017).

In this paper, we investigate how male and female body size—both determined by the early-life environment—interact in determining reproductive success. Our experiments focus on burying beetles Nicrophorus vespilloides. Burying beetle pairs breed on the carcasses of small vertebrates, which they convert into an edible nest for their young (Scott, 1998). They strip off the fur or feathers, roll the flesh into a ball and then bury it below ground (Cotter & Kilner, 2010). Parents feed and defend their larvae until development ends when larvae crawl away into the soil to pupate (Eggert et al., 1998). Burying beetles are holometabolous insects, which means that the adult body is built solely from resources acquired whilst a larva (Hopwood et al., 2013). Larval size at dispersal thus strongly predicts adult size, and there is virtually no genetic heritability in adult size for either sex (Jarrett et al., 2017).

Adult size determines whether beetles win contests for a carcass and this, in turn, influences their social status (Hopwood et al., 2016; Otronen, 1988). There is often significant competition for gaining control of a carcass for breeding: Müller et al. (2007) found up to six male and six female burying beetles present on a 25 g carcass at one time. The larger winning male and winning female become the socially dominant pair and take ownership of the carrion for their own reproduction (Müller et al., 2007). The smaller losers become socially subordinate and pursue alternative mating tactics: subordinate females become intraspecific brood parasites of the dominant female while subordinate males sneak copulations with the dominant female (Müller et al., 2007). As described above, males also adopt different fertilization tactics, according to their size and social status, with smaller subordinate males being more capable of stimulating female fecundity (Pascoal et al., 2018).

In addition, adult size influences female fecundity. Larger females lay more eggs (Jarrett et al., 2017; Steiger, 2013), the eggs are larger than those laid by smaller females (Richardson & Smiseth, 2019), and they produce heavier larvae (Steiger, 2013). Larger females are also more inclined to practice partial filial cannibalism (Bartlett & Ashworth, 1988; Jarrett et al., 2017). In short, there is considerable scope for the early-life environment experienced by females to interact with the early-life environment experienced by her mates to jointly influence each party's reproductive success—through their combined effects on fecundity, sperm competition, parental care and the capacity for eliminating surplus offspring.

We investigated such interactive effects by testing the following specific predictions: (1) When they mate first, small males stimulate female fecundity to a greater extent than larger males (as previously shown in Pascoal et al., 2018), even when females are drawn from a large size range. (2) When small males mate first with large females, they induce those females to produce disproportionately more eggs than if the females were small. (3) Large females influence the paternity obtained by males that mate second to a greater extent than small females because they are physically more capable of resisting unwanted matings. Note that, due to space constraints, we have
abbreviated these predictions to questions in the remainder of the paper.

2 | METHODS

2.1 | General beetle husbandry

The *N. vespilloides* stock population used for the experiments was established with beetles captured from three sites in Cambridgeshire, UK (Byron’s Pool, Gamlingay Woods and Waresley Woods). They were interbred in the laboratory for two generations before the experiment began. Adult beetles were kept in individual clear plastic boxes (12 × 8 × 6 cm) filled with moist soil and fed twice weekly on raw beef mince. To ensure that all experimental beetles were sexually mature, adults were paired at 17 days after eclosion in clear plastic breeding boxes (17 × 12 × 6 cm) containing a layer of moist soil and a mouse carcass. Breeding boxes were then kept in a dark cupboard at 21°C, to simulate natural breeding conditions underground. Eight days after parental pairing, larvae started to disperse away from the scant remains of the carcass. At this point, we placed larvae from each brood in the individual cells (2 × 2 × 2 cm) of a clear plastic eclosion box (10 × 10 × 2 cm) and filled the box with moist peat. Here, the larvae pupated and then eclosed as adults approximately 21 days later. We kept both individual and eclosion boxes on a 16L:8D hour light cycle at 21°C.

2.2 | Generating experimental individuals

We used Steiger (2013)’s technique for engineering larvae of different sizes. We began by pairing unrelated virgin male and virgin female burying beetles from the laboratory stock population. Pairs were placed in breeding boxes containing a 10–12 g mouse carcass and constant amount of soil, and left in a darkened chamber to mate, prepare the carcass, lay eggs and begin to provision their offspring. Five days after pairing, half of each pair’s larvae were removed from the carcass and placed directly in eclosion boxes. This early removal, before natural dispersal, prevented further food consumption by larvae and eventually yielded small adults (Pascoal et al., 2018; Steiger, 2013). The larvae that were left on the carcass at this time were subsequently removed at the natural dispersal time (8 days after pairing), were larger at the end of larval development and consequently matured into larger beetles. Larvae that were removed after 8 days were transferred to different eclosion boxes than those that were removed at 5 days. After eclosion, all beetles were temporarily anaesthetized with carbon dioxide and photographed individually using a mounted camera, and with a scale bar in the image. The pronotum width of each beetle was digitally measured using ImageJ (Schneider et al., 2012), and we discarded beetles which were of intermediate size (defined as those with pronotum widths greater than 4.7 mm and less than 5.3 mm). ‘Small’ beetles were those with a pronotum width greater than 3.2 mm and less than 4.7 mm, while ‘large’ beetles were those with a pronotum width greater than 5.3 mm and less than 6.1 mm (n = 120 females and 240 males). Only beetles within the natural range found in the wild (Pascoal et al., 2018) were used, and similar size ranges were used for both male and females as there is no sexual size dimorphism in the species.

2.3 | Predictions (1) and (2): Are small males better at stimulating female fecundity and can they disproportionately induce larger females to lay more eggs than smaller females?

The ‘small’ and ‘large’ beetles (as determined using the criteria above) were divided into eight treatment groups: SLL, SSS, SLS, SSL, LLL, LSS, LLS and LSL (where the first letter denotes the size of the female and the second two letters denote the size and sequence of the males with whom she was successively mated: L = large, S = small,

![FIGURE 1](image-url)  
**FIGURE 1** Experimental design. Each treatment is described by giving the size of the female first, then the size of the 1st male to mate with her, followed by size of the 2nd male. L, large beetle; S, small beetle
Figure 1). Within each experimental trio, all individuals were unrelated virgins and were derived from a unique combination of broods to prevent any confounding effects attributable to the family of origin.

For mating trials, the female was placed in a breeding box with the first male for 24 hr, after which the first male was removed and replaced with a second male, which remained with the female for a further 24 hr. When the second male was removed, the female was given a 10–12 g mouse carcass for breeding (adults also feed on the carcass a little). Removing males before presenting the carcass eliminated any potential confounding effects of paternal care on measures of reproductive success.

We counted the number of eggs the female laid by inspecting the underside of the box 53 hr after giving a female a carcass. This technique for estimating clutch size is the least disruptive to the burying beetle and most likely to ensure high hatching success (Sun et al., 2020). Previous studies have shown a strong positive correlation between the number of eggs visible on the underside of the breeding box and the total number of eggs laid (Jarrett et al., 2017; Monteith et al., 2012; Schrader, Cosby, et al., 2015). Females were then left alone to raise their larvae. Eight days after being given a mouse, the larvae started to disperse away from the remains of the carcass. At this point, we counted and weighed them. Both parents and offspring were then preserved in absolute ethanol in preparation for paternity analysis.

2.4 | Prediction (3): Does female size influence male P2 scores?

DNA extractions and parentage analyses were conducted on 20 randomly chosen families from treatments where the males differed in size (n = 20 females, 40 males and 526 offspring), following the protocols detailed in Pascoal et al. (2018). We were unable to analyze more families than this due to logistic constraints. Total genomic DNA was extracted from each beetle’s head and pronotum using the DNeasy Tissue Kit (Qiagen) in accordance with the manufacturer’s instructions. The Qiagen Multiplex PCR kit was used to amplify one microsatellite multiplex with five microsatellite markers (Pascoal & Kilner, 2017). Fragment analysis was performed on an ABI 3730 instrument at the Edinburgh Genomics Institute Sanger Sequencing Centre with GeneScan 500 LIZ (Applied Biosystems) as internal size standard. Alleles were scored using Peak Scanner v.1.0 (Applied Biosystems) and CERVUS (Kalinowski et al., 2007) was used to assign parentage.

2.5 | Statistical analyses

All statistical tests were conducted in R version 3.6.1 (R Development Core Team, 2020) and a .05 significance threshold was used throughout. All analyses included only those broods which produced at least one surviving larva (n = 116 out of 120 pairs originally used).

As there was no overlap between the sizes of males and females in the small and large size categories, size was conservatively coded as a two-level factor rather than as a continuous variate (Figure S3). Effects of male and female size on clutch and brood size, and average larval mass, were each analyzed using linear models with Gaussian error structures and a step-down method (where the term with the highest p-value was removed from each model sequentially until a minimal model was reached where only terms with significant p-values remained) was used to determine significance of each term. The interactions between the sizes of the female and each male, and the two males, were also included as covariates in the models, as was the mass of the mouse carcass on which they bred, as this has been shown to affect clutch and brood size (Trumbo, 1992). In the analysis of average larval mass, brood size was also included, since maternal provisioning per larva is proportionally reduced in larger broods (Bartlett & Ashworth, 1988).

To determine whether mating order affects percentage of paternity, as we had found before (Pascoal et al., 2018), we first ran two paired t tests with the numbers of offspring sired by small males compared to those sired by large males, and the numbers of offspring sired by the first compared to the second male to mate. We then ran two quasi-binomial linear models, first with the proportion of offspring sired by the second male to mate (P2) as the response variable and, second, with the proportion of offspring sired by the large male as the response. In both models, female size and second male size were included as explanatory variables. Due to logistic constraints, we only tested broods where the males were different sizes. Therefore, it was not possible to run a linear model with paternity as a response and the sizes of the female and both males as the explanatory variables, because we did not have paternity data for every combination of male sizes. Using these three models together we could determine whether size or mating order alone affected paternity (the t tests), whether P2 was affected by the second male’s size (the linear model with P2 as the response) and whether the mating sequence position of the large male made it any more likely that he would dominate the paternity share (the linear model with large male paternity as the response).

3 | RESULTS

3.1 | Prediction (1): Do small males stimulate female fecundity more than large males?

We found that female body size was the strongest predictor of clutch size (Table 1A, Figure 2a). After controlling for female size, there was a trend for small males to increase the number of eggs laid by females but it was not statistically significant (F_{1,113} = 3.84, p = .053; Table 1A). Turning to brood size, we found that large females produced more dispersing larvae than small females (Table 1B, Figure 2b). We found no evidence that male size affected the number of larvae produced (Table 1B).
3.2 | Prediction (2): Are large females disproportionately more affected by small first males’ fecundity stimulation compared to small females?

There was no significant effect of large females laying disproportionately more eggs than small females after mating with a small male first \( F_{2,112} = 2.10, p = .127 \); Female size:Male 1 size interaction term, Table 1A). We found no evidence that large females produced disproportionately more dispersing larvae than small females when mated first with small males (Female size:Male 1 size interaction term, Table 1B).

As our results in Prediction 1 showed that there was an association between brood size and female size, we generated a Variance Inflation Factor (VIF) for each term in our average larval mass model,
to ensure that there was not excessive covariance (Zuur et al., 2010). No VIFs exceeded 3.01, and therefore, we proceeded with including both terms in the model. Average larval mass at dispersal was strongly and negatively associated with brood size at dispersal (Table 2, Figure 3). However, the slope of this relationship differed among treatments (Table 2, Figure 3). We found that dispersing larvae attained a greater mass when raised by a large female which had mated first with a small male (Female size: Male 1 size interaction term, Table 2, Figure 3).

### 3.3 Prediction (3): Does female size influence male P2 scores?

Paternity could reliably be assigned to larvae from 19 of the 20 families; therefore, only these families were included in the analyses of parentage. Absolute paternity was not significantly affected by either male size ($t = 0.7$, $df = 18$, $p = .496$) or mating order ($t = -1.66$, $df = 18$, $p = .115$). Neither female size nor the size of the second male to mate significantly affected the proportion of a brood’s offspring sired by the second male (Table 3A). Likewise, neither female size nor the size of the second mating male affected the paternity obtained by the large male (Table 3B).

### 4 DISCUSSION

The goal of this study was to investigate how early-life conditions of mates interact to influence reproductive success. We were particularly interested in early-life effects mediated by body size, and how early-life effects interact when females mate with more than one male during each breeding event. Specifically, we sought to determine whether larger females are more susceptible to fecundity stimulation by small males compared to small females, and whether female size influences the ability of her mates to compete for paternity.

We did not find significant support for Prediction (1) (*small males stimulate female fecundity more than large males*), but the direction of the trend was the same as in Pascoal et al. (2018): females were induced to lay larger clutches when their first mate was a small male. The mechanism by which small males stimulate female fecundity remains unclear. While burying beetles offer no pre-copulatory gifts and do not perform any courtship displays, it is possible that smaller males have a different seminal fluid composition (Wigby & Chapman, 2005; Yamane et al., 2015) and this is the subject of ongoing research.

Turning to Prediction (2) (*small males induce large females to lay disproportionately more eggs compared to small females*), we found that larger females laid larger clutches and had larger broods at dispersal than small females, just as has been found in previous work (Bartlett & Ashworth, 1988; Pascoal et al., 2018; Steiger, 2013). However, we found no evidence that small males were able to stimulate large females to lay disproportionately more eggs than small females. Nor did we find that small males induced large females to produce disproportionately more larvae. This prediction was based on the finding from Pascoal et al. (2018) that females of different sizes were seemingly differentially susceptible to the fecundity stimulation properties of small males. However, in Pascoal et al. (2018) female size was experimentally confined to a very narrow range, and only slightly overlapped in size with the large and small females used in this study (see Figure S4). This study used a much greater range of female size and found no equivalent effect. We suggest that any effects on female fecundity detected in Pascoal et al. (2018) were overwhelmed by the much larger effect of female size on clutch size.

We found no evidence to support Prediction (3) either (*large females have a greater influence of second-mate paternity scores than do smaller females*). It is possible that we did not assign paternity

| Independent variable | Estimate | Standard error | F   | Degrees of freedom | p-Value |
|----------------------|----------|----------------|-----|---------------------|---------|
| Intercept            | 0.197    | 0.006          |     |                     |         |
| Carcass mass (g)     | 0.003    | 0.002          | 1.32| 1                   | .254    |
| Brood size           | -0.003   | < 0.001        | 184.37| 1                   | <.001   |
| Female size          | -0.003   | 0.004          | 15.45| 1                   | <.001   |
| Male 1 size          | 0.011    | 0.004          | 1.23| 1                   | .270    |
| Male 2 size          | -0.002   | 0.003          | 0.70| 1                   | .403    |
| Female size:Male 1 size | -0.016 | 0.005         | 9.77| 1                   | .002    |
| Female size:Male 2 size | 0.004   | 0.005         | 0.66| 2                   | .519    |
| Male 1 size:Male 2 size | -0.006 | 0.005        | 0.99| 2                   | .374    |

Note: All terms included in the maximal model are shown, as well as their contribution to the final model that contained them. For female and male size terms, the statistics for the ‘small’ categories are listed. Terms retained in the minimal model are shown in bold. ‘:’ represents an interaction between terms.
FIGURE 3  The relationship between brood size and average larval mass, as influenced by the size of the female and first male to mate. Average larval mass is greater, in relation to brood size, when the female is large and her first mate is small (green points and line) (Table 2). Points show individual breeding pairs (n = 116, 30 LL, 28 LS, 29 SL, 29 SS). Colours of points and lines indicate the combination of the size of the female and first male in those pairs. Shaded areas represent the 95% confidence intervals.

TABLE 3  Results of quasi-binomial linear models analysing predictors of (A) the proportion of offspring in each brood sired by the second male to mate (P2) and (B) the proportion of offspring in each brood sired by the large male (only broods where one large male and one small male mated were included in the analyses).

| Independent variable | Estimate | Standard Error | χ² | Degrees of freedom | p-Value |
|----------------------|----------|----------------|----|--------------------|---------|
| (A) Dependent variable = Proportion of offspring sired by second male | | | | | |
| Intercept            | 0.40     | 0.25           |    | 1                  | .194    |
| Female size          | 0.63     | 0.49           | 10.61 | 1                | .194    |
| Male 2 size          | 0.25     | 0.50           | 1.64 | 1                 | .618    |
| (B) Dependent variable = Proportion of offspring sired by large male | | | | | |
| Intercept            | −0.18    | 0.25           |    | 1                  | .119    |
| Female size          | 0.16     | 0.52           | 0.70 | 1                 | .755    |
| Male 2 size          | −0.78    | 0.50           | 16.60 | 1                | .119    |

Note: For female and male size terms, the statistics for the ‘small’ categories are listed. All terms included in the maximal model are shown, as well as their contribution to the final model that contained them.

to a sufficiently large number of broods to be able to detect an effect of female size on P2. We were also unable to replicate Pascoal et al. (2018)’s finding that large males obtain a higher P2 score than small males, despite using the same method for determining paternity. This might be because the sample size in this study (n = 19 broods) was too small to detect effects of adult size on P2 scores (unlike the larger sample, n = 102 broods, in Pascoal et al., 2018). It should also be noted that there is a general lack of consistency regarding the effect that adult size has on P2, but this is likely due to vastly different methods of measuring paternity (House et al., 2007; Müller & Eggert, 1989; Pettinger et al., 2011; Sakaluk & Müller, 2008).

In natural populations, larger male burying beetles are more likely to be able to mate more with females (Eggert, 1992; House et al., 2007; Müller et al., 2007), and to mate last with dominant females (Pettinger et al., 2011). Our experiments, and those of Pascoal et al., 2018, reduced any size-related variation in male mating opportunity by allowing all males to mate with females repeatedly, and unchallenged, for 24 hr. Therefore, it is still possible that larger males mated with larger females have higher P2 scores, but that any size-related interaction is mediated by behavioural differences, which we did not investigate, in addition to the intrinsic physiological differences which were the focus of our experiment. Indeed, in general, our experiments eliminated most size-related variation in male behaviour, including in their ability to compete directly with each other. These effects remain to be investigated in future work.

Despite finding little support for Predictions (2) and (3), we found some support for the general premise that the early-life environments of males and females can interact to determine reproductive success. One unexpected experimental result was the finding that large females produce heavier larvae at dispersal if they mate first with a small male, rather than a large male (Figure 3). The result was unexpected because we standardized the size of the dead mouse that females bred upon and found females in each treatment produced a similar number of larvae (Table 1B). Therefore, it cannot be explained by differences between treatments in either resource availability or competition among larvae for food (Schrader, Jarrett, et al., 2015).
A potential explanation is that small males induced females to produce more eggs (Table 1A, Pascoal et al., 2018), and large females were then more inclined to cannibalize any surplus offspring (Jarrett et al., 2017). By feeding on surplus larvae instead, larger females may have consumed less carrion leaving more food for each of their surviving larvae, particularly as larvae compete not only with one another to consume the limited resources on the carcass (Pilakouta et al., 2016; Smiseth et al., 2007; Smiseth & Moore, 2008), but also with their parents (Boncoraglio & Kilner, 2012). Whether this explanation is correct remains to be tested in future work, for example by removing females shortly after all eggs have hatched.

Nevertheless, if this filial cannibalism explanation holds, then male stimulation of female fecundity results in the production of extra young that function as resource packages for the female, as homegrown nuptial gifts (Gwynne, 2007; Lewis et al., 2014) rather than units of reproductive success. As long as females consume offspring at random with respect to paternity, it means that the benefits of fecundity stimulation are spread relatively evenly between the sires of the brood and the female, as all parties gain from the production of larger, fitter offspring. It also means the costs are divided more fairly between the sexes. Partial filial cannibalism by females increases the cost of fecundity stimulation for males, because they lose offspring as nourishment to the female, but reduces the burden on females in the sense that, within the same reproductive event, they can recoup some of the costs associated with producing extra larvae. If female fecundity stimulation by males increases the scope for sexual conflict (Wigby & Chapman, 2005), then partial filial cannibalism by females potentially reduces it. Although we propose this hypothesis specifically in relation to burying beetles, it could potentially apply to any other species in which males stimulate female fecundity, at a cost to females, and where females practise partial filial cannibalism.

In summary, we found some indication that the conditions experienced in early life by males and females interact to determine their reproductive success, though not in the ways we predicted. In general, our results suggest such interactions are likely when early-life effects influence adult body size, where adult body size influences social status and where females mate with multiple males who may be socially dominant or subordinate. Our results suggest that when small males mate with large females, their greater stimulation of female fecundity could generate a subset of offspring that are destined to become food for their mother. The challenge for future work is to test this novel hypothesis for the stimulation of female fecundity by males and deduce the implications for sexual conflict.

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Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0cfxpw0c (Bladon et al., 2020).

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