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Food-deprivation affects egg laying and maternal care but not offspring performance in a beetle

Running title: Food deprivation affects reproduction but not offspring performance

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Abstract

Individuals vary with respect to their nutritional state and such variation is an important determinant of the amount of resources individuals allocate towards reproductive functions. Currently, we have a relatively poor understanding of the downstream consequences of food deprivation on different traits associated with reproduction. Here, we address this gap by investigating how food deprivation affected different traits across the breeding cycle in the burying beetle, *Nicrophorus vespilloides*; a species that breeds on carcasses of small vertebrates serving as food for both parents and offspring. We found that food-deprived females took longer to start egg laying than control females, which may allow them more time to feed from the carcass. There was no difference between food-deprived and control females in the number, size, laying pattern or hatching success of eggs, suggesting that this delay allowed females to compensate for their poor initial state. However, food-deprived females spent less time providing care, suggesting that this compensation was incomplete. Finally, we found no evidence for negative effects of food deprivation on the offspring's growth or survival, which is surprising given that food-deprived females took longer to initiate egg laying and provided less care to their offspring. Our results highlight that food deprivation can have complex effects on parental and offspring traits, and suggest that females face a trade-off between the benefits of mitigating downstream consequences of nutritional stress and the costs associated with delaying the start of reproduction.

Keywords: egg laying, nutritional state, offspring begging, offspring performance, parental care, reproductive investment

Introduction

Animals must forage for nutrients to obtain resources for investment into reproduction or other life history functions. Access to nutrients can vary spatially and temporally, leading to variation between individuals in nutritional state. Such variation has important implications because it generates variation in the amount of resources individuals can allocate towards reproductive functions. Individuals deprived of food will have fewer resources to invest than well-fed individuals, and the former might therefore produce fewer and smaller eggs and provide less care for their offspring with detrimental consequences for their offspring's performance. In support of this, there is evidence that nutritional stress has negative effects on traits associated with reproduction in mammals (Atkinson & Ramsay 1995; Koskela et al. 1998; Persson 2005), birds (Clifford & Anderson 2001; Nagy & Holmes 2005; Zanette et al. 2006), fishes (Townshend & Wootton 1985; Tierney et al. 2009; Segers 2011), reptiles (Warner et al. 2007) and arthropods (Kreiter & Wise 2001; Kyneb & Toft 2006; Wong & Kölliker 2012). Furthermore, there is evidence that food deprivation in parents has a negative impact on the offspring's growth, body size and survival (e.g., Keech et al. 2000; Laurien-Kehnen & Trillmich 2004; Salomon et al. 2011; Kramer et al. 2017). Thus, there is good evidence that variation in the nutritional state of parents is a key determinant of variation in traits associated with reproduction as well as in offspring performance.

Currently, we have a relatively poor understanding of downstream consequences of food deprivation on suites of traits associated with reproduction. Most prior work has focused on a relatively limited number of traits associated with reproduction (e.g. Hörnfeldt & Eklund 1990; Clifford & Anderson 2001; Richardson & Smiseth 2019a). However, in many species, reproduction involves complex suites of traits expressed in both parents and offspring. Thus, investigating the downstream consequences of food deprivation on complex suites of traits may provide valuable insights into the mechanisms by which food deprivation affects reproduction. Firstly, the effects of food deprivation at the onset of reproduction may depend on when in the breeding cycle traits are expressed. This might be expected in species where the nutritional state of parents either deteriorates or improves over time. For example, in species where parents acquire resources prior to breeding that serve as food for both parents and offspring, such as necrophagous or parasitoid insects (e.g., Heimpel & Rosenheim 1995; Scott 1998), parents may buffer against initial differences in their nutritional state by feeding from the shared resource, in which case food deprivation may have little or no effect beyond traits expressed at the very beginning of breeding. Secondly, the effects of food deprivation may depend on the extent to which traits are energetically costly. For example, if parents can buffer against initial differences in their nutritional state, but such buffering is incomplete, food deprivation may have a stronger effect on traits that are more energetically costly even though they are expressed at different times in the breeding cycle. Finally, food deprivation of parents may have a detrimental impact on the offspring's performance in species where offspring are dependent on their parents. Furthermore, in species where offspring beg for food from their parents, food deprivation may even alter the offspring's begging behaviour by reducing their nutritional state (Bateson 1994; Kramer & Meunier 2016). Thus, to advance our understaninding of how food deprivation of parents affects reproductive traits, and ultimately offspring performance, there is now a need for studies on species where (1) females have the potential to buffer against effects of food deprivation, and (2) reproduction involves a complex suite of traits expressed at different times during the breeding cycle in both parents and offspring.

Here we use the burying beetle *Nicrophorus vespilloides* to test for differential effects of food deprivation at the onset of reproduction on reproductive traits across the breeding cycle. Burying beetles of the genus *Nicrophorus* are a suitable system for addressing this question because they breed on the carcasses of small vertebrates that serve as a source of food for parents and offspring. As such, females could buffer against the effects of food deprivation by feeding from the carcass. In addition, reproduction involves a complex suite of parental and offspring behaviours and life history traits that are easy to measure and that are separated in time throughout the breeding cycle. Females lay eggs in the soil surrounding the carcass, and eggs hatch asynchronously over a period of 16–56 hours (Müller & Eggert, 1990; Smiseth et al. 2006). Thus, it is straightforward to assess investment during egg laying by measuring the number, size, hatching success and temporal laying pattern of eggs. After hatching, larvae crawl to the carcass and start feeding inside a crater cut into the carcass by the parents. Parents provide care by provisioning food to the larvae and maintaining the carcass as a food source by applying antimicrobial secretions to the external surface (Scott 1998; Arce et al. 2012; Andrews et al. 2016), and larvae beg for food from their parents (Smiseth et al. 2003). These reproductive traits have important consequences for offspring performance as increased hatching asynchrony negatively affects offspring growth and survival (Ford & Smiseth 2016; Ford & Smiseth 2018), whilst greater investment in parental care improves offspring growth and survival (Andrews et al. 2016). Prior work shows that nutritional state has important consequences for reproduction as food-deprived females lay fewer eggs (Steiger et al. 2007), and have fewer adult offspring (Gray et al. 2018; Richardson & Smiseth 2019a). However, there is a lack of information on how food deprivation influences suites of reproductive traits that are expressed at different times in the breeding cycle and in both parents and offspring. In particular, there is a need to understand how food deprivation influences egg laying patterns and post-hatching behavioural traits, such as parental care and offspring begging. Understanding how food deprivation affects these and other traits across the breeding cycle will advance our understanding of the potential mechanisms by which the nutritional state of parents influences offspring performance.

Our aim was to test for effects of food deprivation on suites of traits associated with reproduction in burying beetles. We deprived females of food prior to breeding and monitored subsequent effects on reproductive traits during egg laying (clutch size, egg size, hatching success, time until start of egg laying, and the temporal spread and skew of egg laying) and post-hatching care (time spent provisioning offspring, time spent consuming carrion, and time spent maintaining the carcass by females, and time spent begging by larvae). We also examined the consequences for offspring performance by recording larval growth and survival, and for female performance by recording female mass change during breeding and female lifespan. We predicted that nutritional stress would negatively affect reproductive traits because food-deprived females have fewer resources to invest in reproduction. If females buffer against the effects of food deprivation by feeding from the carcass prior to reproduction, there should be a strong negative effect on the delay until the start of egg laying. However, we predicted little or no effects on traits that occur later in the breeding cycle, such as egg size, parental care, and offspring begging, given that females can replenish their energy reserves and thereby compensate for the effects of food deprivation. If females are unable to completely buffer against the effects of food deprivation, we predicted negative effects of food deprivation on traits that are costly to express but expressed later in the breeding cycle, such as post-hatching care.

Methods

Origin of study population and animal husbandry

Our experiment used virgin beetles from an outbred laboratory population. We used 9th generation beetles descended from wild-caught beetles collected in Edinburgh, UK. We kept all beetles at 20°C under a 16:8 h light:dark cycle. Nonbreeding adults were housed individually in transparent plastic containers (12 x 8 x 2 cm) filled with moist soil and were fed twice a week on pieces of raw beef (approximately 0.3 g).

Experimental design and procedures

We randomly assigned females to one of two treatments 7 days prior to breeding: food-deprived (n = 44) or control females (n = 48). Food-deprived females received no food for 7 days prior to recieving a carcass to initiate reproduction, whereas control females were fed twice during this period. We deprived females of food at 10 days post-eclosion, which is after females had reached sexual maturity. We did this to ensure that food deprivation did not delay sexual maturation (Hopwood et al. 2013; Richardson & Smiseth 2019b). We used 7 days of food deprivation based on prior work showing that deprivation for this length of time leads to significant weight loss without causing a detectable increase in mortality (Hopwood et al. 2013; Gray et al. 2018; Richardson & Smiseth 2019a,b). There was no difference in the body mass of food-deprived and control females before food deprivation ($t_{1,90}$ = 1.88, p = 0.17). We weighed all females before providing them with a carcass to verify that the 7-day food deprivation treatment caused a decline in female nutritional state (see Results). We later used this measure of pre-breeding mass for each female to estimate mass change during breeding (see below).

On day 6 of the food deprivation treatment, we mated females with an unrelated, virgin male from the stock population. We initiated mating by placing each female in a transparent plastic container (11 x 11 x 3 cm) lined with 0.5 cm of moist soil together with her assigned mate for 24 hours. We used this design to ensure that females received sufficient sperm for fertilizing the eggs, thereby allowing them to breed on their own without male assistance (Botterill-James et al. 2017). We excluded males to remove any confounding effects due to male consumption of the carcass or male assistance in parental care on female or offspring traits (Pilakouta et al. 2016; Keppner et al. 2018). Removal of males does not affect larval survival or growth under laboratory conditions in this species (Bartlett 1988; Smiseth et al. 2005). After mating, we transferred females to a larger transparent plastic container (17 x 12 x 6 cm) lined with 1 cm of moist soil, whilst discarding all males. To initiate breeding, we provided females with a freshly thawed mouse carcass (Livefoods Direct Ltd., Sheffield, UK) weighing between 8–10 g (mean ± SE = 8.95 ± 0.051 g). This size of carcass is within the range used by this species (1–40 g; Müller et al. 1990). We used relatively small carcasses to ensure that females had ample resources to breed successfully, whilst avoiding an excess of resources that might mask any effects of food deprivation on reproductive traits (Richardson & Smiseth 2019a).

We collected information on egg laying by placing each container on a flat-bed scanner (Canon CanoScan 9000F Mark II, Canon Inc., Tokyo, Japan) and scanning the bottom every hour until the completion of oviposition using VueScan professional edition software (Hamrick Software, Sunny Isles Beach, Florida, USA) (Ford & Smiseth 2016, Ford & Smiseth 2017; Botterill-James et al. 2017; Ford et al. 2018). Eggs are visible at the bottom of the container and, because we filled containers with a thin layer of soil, the visible number of eggs is strongly correlated with the actual clutch size (Monteith et al. 2012). From each scanned image, we counted the number of new eggs laid each hour, using this information to determine the start of egg laying (i.e., the time elapsed since the female received a carcass until the female laid the first egg), laying spread and laying skew (see below) and clutch size (i.e., the number of eggs laid) (Ford & Smiseth 2016).

The laying pattern can be characterised in two ways: ‘laying spread’, defined as the time between the first and last egg being laid (Smiseth et al. 2006; Takata et al. 2015), and ‘laying skew’, defined as the extent to which laying is skewed towards the earlier part of the laying period (Smiseth et al. 2008; Ford & Smiseth 2016). Both characteristics of the laying pattern have important consequences for offspring performance as a greater laying spread and a more negative laying skew negatively affect offspring growth and survival (Ford & Smiseth 2016; Ford & Smiseth 2018). In accordance with prior work, we calculated a laying skew index as $\Sigma\left(\frac{t_i - t_m}{t_m}\right) \times \ p_i$, where t_i is the time interval of a given scan in relation to the start of the laying period, t_m is the middle of the laying period and p_i is the proportion of the total clutch that is laid in a given scan (Smiseth et al. 2008; Ford & Smiseth 2016). Previous work shows that this index is usually negative, indicating that egg laying is skewed towards the first half of the laying period. Thus, values closer to –1 indicate a greater laying skew where a larger proportion of eggs are laid early on, whereas values closer to 0 indicate a lesser laying skew. In addition, we measured the size of five randomly chosen eggs in each clutch using ImageJ (Ambràmoff et al. 2004). For each egg, we measured its length and width in pixels three times. We then converted these measures to metric length (mm), and used the mean length and width to calculate a prolate spheroid volume for each egg (V) as $V = (1/6)\,\pi w^2 L$, where w is width and L the length of the egg, respectively (Berrigan 1991). We checked scans after hatching to record the number of unhatched eggs.

We estimated hatching success by subtracting the number of unhatched eggs from the clutch size to estimate the number of hatched eggs, and dividing the number of hatched eggs by clutch size.

We collected information on female post-hatching parental care and offspring begging by conducting observations on each female and her brood. In this species, post-hatching parental care and offspring begging peaks at 24 h after offspring hatch (Smiseth et al. 2003). We therefore conducted observations on each female as close as possible to 24 h after her first eggs were expected to hatch (on average females were observed 31 ± 0.42 h after hatching of the first egg). We obtained information on expected time of hatching for each brood by taking the time at which females started egg laying and adding 59 h, which is the time taken for eggs to hatch at 20°C (Smiseth et al. 2006). Observations were conducted using instantaneous sampling every 1 min for 30 min in accordance with established protocols (Smiseth & Moore 2002; Smiseth et al. 2003; Smiseth et al. 2005). We recorded female parental behaviour as the number of sampling points out of 30 in which females were (1) provisioning food to the brood, defined as when females engaged in mouth-to-mouth contact with at least one larva, (2) consuming carrion, defined as when females were feeding within the carcass crater, and (3) maintaining the carcass, defined as when females added anal or oral secretions to the external surface of the carcass, excavated the depression in the soil surrounding the carcass, or moved the carcass from below. All other behaviours, such as self-grooming or being away from the carcass, were recorded as non-parental behaviours and not analysed further.

We also recorded the amount of time spent begging by larvae by counting the number of begging larvae in each sampling point. A larva was scored as begging when it raised its head towards the female, waved its legs towards the female, or touched the female with its legs. We calculated the average amount of time spent begging by each individual larvae in the brood (b_i) as $b_i = (\,\Sigma b/l\,) \times (100/d)$, where Σb is the total number of begging events occurring during each observation, l is the number of larvae at the time of observation, and d is the number of sampling points during an observation that the female was within a pronotum width of the brood (approximately 5 mm). This corresponds to the distance from which offspring initiate begging (Rauter & Moore 1999). After the observations, we left females to rear their broods until the larvae dispersed from the carcass approximately 7 days later.

When all larvae had dispersed from the carcass, we recorded the number of dispersing larvae and the total brood mass. We calculated average larval mass at dispersal in each brood by dividing the total brood mass by the number of larvae in the brood. We then placed the larvae from each brood into transparent plastic containers (17 x 12 x 6 cm) filled with moist soil. Approximately 20 days later, we recorded the number of offspring from each brood that successfully eclosed as adults. At the time of dispersal, we also weighed each female to measure her post-breeding mass. We then calculated mass change during breeding for each female by subtracting her pre-breeding mass from her post-breeding mass. Females were then transferred to individual containers (12 x 8 x 2 cm) filled with moist soil and maintained following the protocol for beetles in the stock population (see above) and checked twice weekly until death to record lifespan. All data were collected blind with respect to female nutritional state.

Statistical analyses

We used R version 3.5.1 (R Core Team 2018) for all analyses. We added experimental treatment (food-deprived or control) as a fixed effect in all models. We used general linear models for traits with normally distributed errors (time to start of egg laying, laying spread, laying skew, average egg size, average amount of begging, number of larvae at dispersal, average larval mass at dispersal, number of offspring at eclosion and female mass change). We used generalized linear models for traits with Poisson distributed errors (clutch size), negative binomial distributed errors (female lifespan) or binomial distributed errors corrected for overdispersion (hatching success). In addition, for the analyses of female behaviour (time spent provisioning food to larvae, time spent consuming carrion, time spent maintaining the carcass), we used generalized linear models fitted with a quasibinomial error structure because our count data was bounded at a maximum value of 30 (i.e. the maximum number of sampling points a female could be observed performing a given behaviour) (Ratz & Smiseth 2018).

We included clutch size as an additional covariate in the analyses of laying spread, laying skew and hatching success to control for any effect of variation in the number of eggs laid on the laying pattern or hatching success of eggs. The number of larvae at dispersal was included as an additional covariate in the analyses of female mass change and female lifespan to account for any effect of variation in the number of offspring a female reared on female performance. The decision about whether to include these additional covariates in the analyses of egg laying or female performance were based on comparison of AIC scores between models, and based on this criterion, clutch size was excluded as an additional covariate in the final analyses of egg size and time until the start of egg laying. Meanwhile, the number of larvae in the brood at the time of the observation was included as an additional covariate in the analyses of female behaviour to account for variation in the number of larvae between broods. In addition, we initially included the interaction between clutch size and treatment (food-deprived vs. control) in the analyses of egg laying traits, and the interaction between brood size and treatment for analyses on female behaviour and female performance. There was no effect of this interaction on any traits, and it was therefore excluded from the final models. Although time elapsed from hatching until the observation was not equal for all broods, inclusion of this variable had no effect on any model outputs and it was therefore excluded from the final models. We accounted for multiple testing using a false discovery rate correction (Benjamini & Hochberg 1995). We note there was no change in the interpretation of our results after this correction.

Results

Effects of food deprivation

There was a significant difference between food-deprived and control females in their mass change during the 7-day long food deprivation treatment (estimate = –0.034 ± 0.004 g, $t_{1,89} = -8.38$, $p < 0.001$). As intended, food-deprived females lost mass during food deprivation (mean ± SE: –0.027 ± 0.002 g) whereas control females did not (0.007 ± 0.003 g).

Female egg laying

As expected, food-deprived females delayed the onset of egg laying compared to control females (Table 1). Food-deprived females took on average, 37.1 % longer to begin egg laying than control females (Figure 1). However, there was no significant differences between food-deprived and control females in clutch size, average egg size, hatching success, laying spread or laying skew (Table 1).

Female parental behaviour

Food deprivation had a significant effect on maternal behaviour (Table 2). Food-deprived females spent, on average, 43.9 % fewer sampling points provisioning food to their larvae and 43.1 % fewer sampling points maintaining the carcass than did control females (Figure 2A-B). In addition, food-deprived females spent, on average, 148.8 % more sampling points consuming carrion than did control females (Figure 2C). When caring for a larger number of offspring, females spent more time provisioning food to the brood and more time maintaining the carcass (Table 2). The number of larvae in the brood at the time of observation had no effect on the amount of time females spent consuming carrion (Table 2).

Food-deprived females might spend more time consuming carrion to replenish their own energy reserves or to regurgitate pre-digested carrion to their offspring. To test between these two alternative explanations, we examined the correlations between time spent consuming carrion and time spent provisioning offspring and between time spent consuming carrion and female weight change separately for food-deprived and control females. We found a significant positive correlation between time spent consuming carrion and time spent provisioning food to offspring for control females (Pearson's correlation: $r = 0.28$, $t = 2.02$, $p = 0.048$), but no such correlation for food-deprived females (Pearson's correlation: $r = -0.16$, $t = -1.08$, $p = 0.28$; Figure 3). In contrast, there was a significant positive correlation between time spent consuming carrion and female mass change for food-deprived females (Pearson's correlation: $r = 0.31$, $t = 2.13$, $p = 0.038$), but no such correlation for control females (Pearson's correlation: $r = 0.14$, $t = 0.97$, $p = 0.33$; Figure 3).

Offspring begging behaviour

Food deprivation of females had a significant effect on offspring begging behaviour (Table 2) as larvae reared by food-deprived females spent, on average, 52.2 % more time begging than larvae reared by control females (mean ± SE: 9.68 ± 1.40 vs 6.36 ± 0.42; Figure 2D).

Offspring performance

We found no significant difference between food-deprived females and control females in the number of dispersing larvae, average larval mass at dispersal or the number of offspring at eclosion (Table 3).

Female weight gain and post-breeding performance

There was a significant difference between food-deprived and control females in terms of female mass change over the breeding attempt (Table 3; Figure 4). Food-deprived females gained on average, 3500 % more mass (mean ± SE: 0.035 g ± 0.002) during reproduction than did control females. In addition, there was a significant effect of the number of larvae in the brood at dispersal on female mass change. Females caring for a larger number of offspring gained less mass than females caring for a smaller number of offspring (Table 3). Food deprivation also had a significant effect on the mass of females at larval dispersal (estimate ± SE = 0.021 ± 0.008 g, t = 2.41, p = 0.018), as food-deprived females were 6.7 % heavier (mean ± SE: 0.298 ± 0.0064 g) than control females (0.278 ± 0.0062 g). There was no significant difference between the lifespan of food-deprived females and control females (Table 3).

Discussion

We examined downstream consequences of food deprivation on a complex suite of traits associated with reproduction in the burying beetle *N. vespilloides*; a species where females acquire resources for breeding prior to reproduction and provide elaborate care to their offspring. Females that had been deprived of food for 7 days lost more mass than control females, confirming that food deprivation had caused a deterioration in female nutritional state by the onset of reproduction. Food-deprived females delayed the onset of egg laying for 37.1 % longer than control females. However, food deprivation had no effect on other pre-hatching traits, such as the number, size and hatching success of eggs or the pattern of egg laying. Food-deprived females spent less time provisioning food to their larvae and maintaining the carcass than control females. Food deprivation affected offspring behaviour as larvae of food-deprived females spent more time begging than larvae of control females. Food-deprived females spent more time consuming carrion and gained more weight during breeding. However, there was no difference in the subsequent lifespan of food-deprived and control females and no difference in the number or size of larvae produced by food-deprived and control females. We conclude that, even though food-deprived females consumed more food from the shared resources, they were unable to completely buffer against the effects of food deprivation. Furthermore, even though food-deprived females spent less time providing care for the larvae, there were no detectable effects of food deprivation on offspring performance. Below we provide a more detailed discussion of our results and their implications for our understanding of downstream consequences of food deprivation on different traits associated with reproduction.

As expected, food-deprived females delayed the onset of egg laying compared to control females. In this species, females do not mature their oocytes before finding a carcass (Scott & Traniello 1987), and females feed from the carcass to obtain nutrients for egg production (Wilson & Knollenberg 1984). Thus, this finding suggests that food-deprived females delayed the start of egg laying to spend more time acquiring nutrients to invest in egg production, which is in keeping with prior work on this species (Gray et al. 2018) and the congener *N. orbicollis* (Trumbo & Xhihani 2015). By delaying the start of egg laying, females may replenish their nutrient reserves, thereby allowing them to mitigate any negative consequences of nutritional stress on subsequent traits associated with reproduction. In support of this suggestion, we found no evidence that food deprivation affected other traits associated with egg laying, such as clutch size, egg size, hatching success, laying spread and laying skew. Furthermore, prior work shows that food-deprived females have recovered their lost mass by the time larvae hatch (Trumbo & Xhihani 2015; Gray et al. 2018). Nevertheless, our results contrast with those of a prior study on the same species, reporting that food-deprived females laid fewer eggs than control females (Steiger et al. 2007). A potential explanation for this discrepancy is that the period of food deprivation differed between studies (Steiger et al. 2007: 14 days; our study: 7 days), suggesting that the effects of food deprivation may depend on whether females have been exposed to moderate versus extreme levels of starvation.

Contrary to what we expected if delaying the onset of egg laying allowed females to buffer against the effects of food deprivation, food-deprived females spent less time provisioning food to larvae and maintaining the carcass. This finding suggests that food-deprived females only partially compensated for the effects of food deprivation by delaying the onset of egg laying. There are two potential explanations for why we found a differential effect of food deprivation on traits associated with egg laying (clutch size, egg size, hatching success, laying spread and laying skew) and post-hatching parental care. First, this differential effect may reflect that parental care incurs higher energetic costs than egg laying (Monteith et al. 2012). If so, delaying the onset of egg laying to obtain more nutrients may have allowed food-deprived females to offset the lower costs associated with egg laying but not the higher costs associated with parental care. Second, this differential effect may reflect that nutritional stress triggers an increase in investment in somatic maintenance at the expense of costly post-hatching parental care. Individuals may alter how they prioritise investment in survival versus reproduction based on past experiences of adverse conditions (Cotter et al. 2011; Billman et al. 2014). If so, food-deprived females may have prioritised their own condition to ensure that they had sufficient nutrient reserves to tolerate future starvation. Our results raise the question as to why food-deprived females did not delay egg laying even longer to fully compensate for the effects of nutritional stress? One potential answer is that delaying the start of egg laying for too long is associated with significant costs. For example, in our study species, such a delay is associated with further decomposition of the carcass, which negatively impacts egg survival (Jacobs et al. 2014) and larval growth (Rozen et al. 2008). Thus, food-deprived females may need to balance the benefits of delaying the onset of egg laying to themselves against the costs to their offspring.

Food-deprived females spent more time consuming carrion than control females. In burying beetles, consuming carrion serves a dual purpose: boosting the parent's nutrient reserves for investing in future reproduction (Billman et al. 2014) and providing a source of pre-digested carrion for regurgitation to offspring (Mattey & Smiseth 2015; Pilakouta et al. 2016). Prior work suggests that females regurgitate most of the carrion they consume and that carrion consumption is a form of care (Walling et al. 2008; Pilakouta et al. 2016; Andrews et al. 2016). In contrast, males consume carrion primarily to boost their own reserves (Mattey & Smiseth 2015; Pilakouta et al. 2016). We found a positive correlation between time spent consuming carrion and time spent provisioning food to offspring for control females but not for food-deprived females. In contrast, there was a positive correlation between time spent consuming carrion and weight gain for food-deprived females but not for control females. Taken together, these results suggest that control females consumed carrion primarily to regurgitate pre-digested carrion to their offspring, as suggested by prior work (Mattey & Smiseth 2015; Pilakouta et al. 2016), whilst food-deprived females consumed carrion primarily to boost their own nutrient reserves. In support of this interpretation, food-deprived females gained more weight during breeding and were heavier at the end of breeding than control females. Thus, our results suggest that consuming carrion can be considered a form of parental care for control females but not food-deprived females.

There was no evidence that food deprivation of females influenced offspring performance, as there was no difference between food-deprived and control females with respect to number of dispersing larvae, average larval mass or number of offspring at eclosion. This result is somewhat surprising given that food-deprived females took longer to initiate egg laying and provided less care to their offspring, both of which should negatively affect offspring performance (Ford & Smiseth 2016; Smiseth et al. 2003). Our results also contrast with those of a prior study on the same species, reporting that offspring of food-deprived mothers have reduced fitness (Keppner et al. 2018). These contrasting results may reflect that the prior study examined effects of food deprivation in the context of biparental care, whilst our study examined such effects in the context of uniparental female care. Thus, increased female feeding from the carcass may only have a detrimental effect on offspring in the presence of a male partner, presumably due to sexual conflict over feeding from the shared resource (Pilakouta et al. 2016). There are a number of potential explanations for why we found no evidence for a negative impact on offspring performance. First, the beneficial effects of post-hatching parental care to offspring are small in this species (an increase in time spent providing direct care of 1 sampling point translates to a 1.6 mg increase in larval mass; Andrews et al. 2016). Thus, we may not have had sufficient statistical power to detect such small effects (statistical power of our study for detecting the effect size reported by Andrews et al. (2016): $1–\beta = 0.35$). Furthermore, even if detectable, it is unlikely that such a small effect would be biologically meaningful. To illustrate this, the reduction in time spent provisioning food by an average of 3.18 sampling points by food-deprived females would translate into a decrease in average larval mass by 2.81 %. Second, offspring of food-deprived mothers may compensate for any reduction in parental care by obtaining more nutrients through self-feeding. Such compensation may even be a by-product of food-deprived females consuming more carrion, thereby exposing fresher and/or more nutritious parts of the carcass to the larvae. Third, although food-deprived females provided less parental care, they might have provided higher quality care. For example, given that food-deprived females consumed more carrion, they may have transferred a larger amount of pre-digested carrion during each provisioning event. Finally, parental food provisioning is associated with transfer of bacterial symbionts, which may have important consequences for offspring fitness by improving resistance towards pathogens (Ziadie et al. 2019). However, such benefits may only be apparent when offspring are exposed to harsher conditions with more pathogens than those experienced in a laboratory environment. Thus, one avenue for future work is to examine if food-deprived and control females differ in the type or quantity of bacterial symbionts they transfer to their offspring.

We found no evidence that food-derived females produced fewer offspring than control females. In contrast, two recent studies on *N. vespilloides* reported that food-deprived females have fewer adult offspring than control females, but only when breeding on larger carcasses (i.e. >20 g; Gray et al. 2018; Richardson & Smiseth 2019a). Our results are consistent with this work as we bred females on smaller carcasses (i.e., 8–10 g). Food-deprived females may have fewer offspring on larger carcasses because such carcasses support more microbial growth, which is detrimental to offspring survival (Rozen et al. 2008). In support of this, we found that food-deprived females spent less time maintaining the carcass (i.e. applying anti-microbial secretions). Thus, offspring of food-deprived females may suffer higher mortality on larger carcasses as a result of reduced carcass maintenance. These findings are intriguing because they suggest that the benefits of parental care are greater on larger carcasses. Previous work has assumed that larger carcasses are beneficial as they provide more resources, thereby allowing females to produce more offspring (e.g., Smiseth et al. 2014). However, larger carcasses may also represent a more harmful environment for offspring. Our results have important implications as they suggest that the parent's nutritional state may determine how the benefits of care vary with environmental conditions.

Our study adds to our understanding of downstream consequences of food deprivation by demonstrating that food deprivation can have complex effects on traits associated with reproduction. Firstly, food-deprived females buffered against some of the consequences of food deprivation by delaying the start of egg laying given that food deprivation had no effects on clutch size, egg size, hatching success, laying spread and laying skew. However, this buffering was incomplete as food-deprived females provided less post-hatching parental care than control females. Given that parental care occurred later in the breeding cycle than egg laying, this finding highlights that food deprivation can affect traits regardless of when they occur in the breeding cycle and regardless of whether food-deprived females had regained their initial body mass. Such complex effects would be missed when considering effects on single traits, or traits occurring at one stage of the breeding cycle. Thus, we encourage future work to examine effects on suites of traits in species where reproduction involves traits that are expressed at different times during the breeding cycle and that include both parental and offspring traits. Our results also suggest that, when females compensate for the effects of food deprivation, there is a trade-off between the benefits of mitigating downstream consequences of nutritional stress and the costs associated with delaying the start of reproduction. Such a trade-off is likely to be ubiquitous, but the factors that influence how individuals balance these benefits and costs may vary both between and within species. Such variation may depend on how effectively parents mitigate the downstream consequences, how detrimental the costs of delaying reproduction are to offspring, as well as a range of additional factors such as the parent’s state (e.g. age or inbreeding) and environmental conditions (i.e. competition or resource availablity). Future work in this field should now consider examining factors that influence trade-offs in reproductive decision-making and the consequences this has for reproduction.

Finally, we found no evidence that offspring suffered fitness consequences when reared by a food-deprived mother, despite such females delaying the onset of reproduction and providing less parental care. This finding contrasts with prior work on a variety of other species, reporting that offspring suffer fitness costs when reared by a food-deprived mother (e.g., Keech et al. 2000; Laurien-Kehnen & Trillmich 2004; Salomon et al. 2011; Kramer et al. 2017). This finding suggests that detrimenral effects to offspring are not inevitable, presumbably reflecting that parents and/or offspring adjust their behaviour to compensate for the detrimental effects of food deprivation. Given how important offspring growth is for fitness in this species (Otronen 1988), there is likely to be strong selection on mechanisms that compensate for any detrimental effects due to reduced parental care. Such mechanisms could include increased self-feeding by offspring as well as increased investment to parental care by the partner when females are assisted by a partner. Future work should examine the role such mechanisms play in compensating for the effects of parental food deprivation on offspring performance.

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Data accessibility

Analyses reported in this article can be reproduced using the data provided by Richardson et al. 2019.

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Figure legends

Figure 1 – Effect of food deprivation on the time taken (hours) from being provided with a mouse carcass to the time the first egg was laid. Smaller grey points represent each individual brood. Larger black points represent the mean (± SE) for each treatment.

Figure 2 – Effect of food deprivation on the number of sampling points (out of 30) that females spent provisioning offspring (A), maintaining the carcass (B), and consuming carrion (C) and the average time spent begging by offspring (D). Behaviour was recorded using instantaneous sampling every 1 minute for 30 minutes. Smaller grey points represent each individual female or brood. Larger black points represent the mean (± SE) for each treatment.

Figure 3 – Relationship between (A) time spent consuming carrion and female mass change and (B) time spent consuming carrion and time spent provisioning food to offspring. Black points and lines (± 95% CI) represent data on food-deprived females whilst grey points and lines (± 95% CI) represent data on control females.

Figure 4 – Effect of food deprivation on female mass change (g) over the breeding attempt. Smaller grey points represent each individual female. Larger black points represent the mean (± SE) for each treatment.

Table 1 – Effects of female nutritional condition (control or food-deprived) on egg laying. We provide parameter estimates (± SE), test statistics, p-values and means (± SE) for control and food-deprived females.

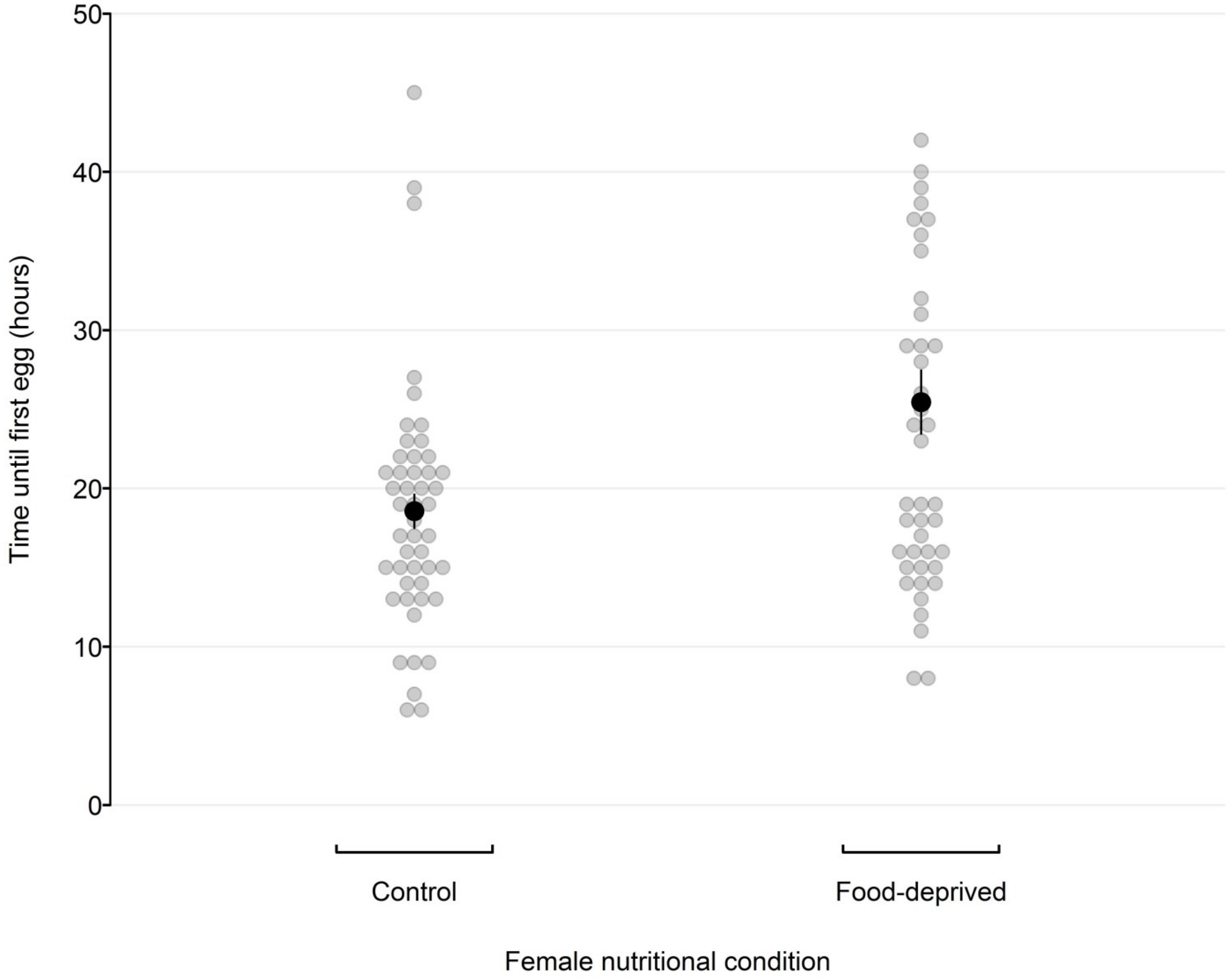
	Effect of female nutritional condition			Effect of clutch size			Mean ± SE for control females	Mean ± SE for food-deprived females
	Estimate ± SE	Test statistic	p-value	Estimate ± SE	Test statistic	p-value		
Time until start of laying (h)	6.89 ± 2.29	t = 3.01	**0.003**	–	–	–	18.60 ± 1.12	25.50 ± 2.05
Laying spread (h)	2.67 ± 2.81	t = 0.95	0.34	-0.05 ± 0.18	t = -0.29	0.77	28.70 ± 1.40	31.50 ± 2.46
Laying skew	0.01 ± 0.05	t = 0.31	0.76	-0.001 ± 0.003	t = -0.27	0.79	-0.262 ± 0.033	-0.244 ± 0.036
Clutch size	-0.06 ± 0.04	t = -1.73	0.08	–	–	–	27.70 ± 1.11	25.90 ± 1.09
Egg size (mm^3)	-0.02 ± 0.05	t = -0.65	0.52	–	–	–	1.75 ± 0.032	1.72 ± 0.033
Hatching success (%)	-0.52 ± 0.40	t = -1.29	0.19	0.01 ± 0.03	t = 0.37	0.71	95.40 ± 1.33	94.4 ± 1.30

Table 2 - Effects of female nutritional condition (control or food-deprived) on female post-hatching care and offspring begging. We provide parameter estimates (± SE), test statistics, p-values and means (± SE) for control and food-deprived females.

	Effect of female nutritional condition			Effect of brood size at time of observation			Mean for control females ± SE	Mean for food-deprived females ± SE
	Estimate ± SE	Test statistic	p-value	Estimate ± SE	Test statistic	p-value		
Time spent provisioning larvae (sampling points)	-0.68 ± 0.13	t = -4.94	**<0.001**	0.04 ± 0.009	t = 4.39	**<0.001**	7.25 ± 0.52	4.07 ± 0.40
Time spent consuming carrion (sampling points)	1.17 ± 0.18	t = 6.17	**<0.001**	-0.01 ± 0.01	t = -0.94	0.35	4.10 ± 0.45	10.20 ± 0.88
Time spent maintaining carcass (sampling points)	-0.65 ± 0.17	t = -3.69	**<0.001**	0.03 ± 0.01	t = 3.01	**<0.001**	6.40 ± 0.60	3.64 ± 0.41
Mean begging by offspring	3.31 ± 1.41	t = 2.34	**0.021**	–	–	–	6.36 ± 0.42	9.68 ± 1.40

Table 3 - Effects of female nutritional condition (control or food-deprived) on female mass change and lifespan as well as on offspring performance. We provide parameter estimates (± SE), test statistics, p-values and means (± SE) for control and food-deprived females.

	Effect of female nutritional condition			Effect of brood size at dispersal			Mean for control females ± SE	Mean for food-deprived females ± SE
	Estimate ± SE	Test statistic	p-value	Estimate ± SE	Test statistic	p-value		
Female mass change during breeding (g)	0.03 ± 0.005	t = 6.29	**<0.001**	-0.001 ± 0.0005	t = -2.93	**0.004**	0.001 ± 0.003	0.036 ± 0.005
Female lifespan (days)	-0.04 ± 0.07	t = -0.54	0.59	0.003 ± 0.005	t = 0.57	0.56	109 ± 5.6	105 ± 5.0
Number of dispersing larvae	-0.85 ± 1.24	t = -0.68	0.50	–	–	–	14.40 ± 0.79	13.50 ± 0.96
Mean larval mass at dispersal (g)	-0.003 ± 0.009	t = -0.29	0.77	–	–	–	0.181 ± 0.006	0.173 ± 0.007
Number of offspring at eclosion	-0.60 ± 1.21	t = -0.49	0.62	–	–	–	13.60 ± 0.80	13.00 ± 0.94


50
40
30
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10
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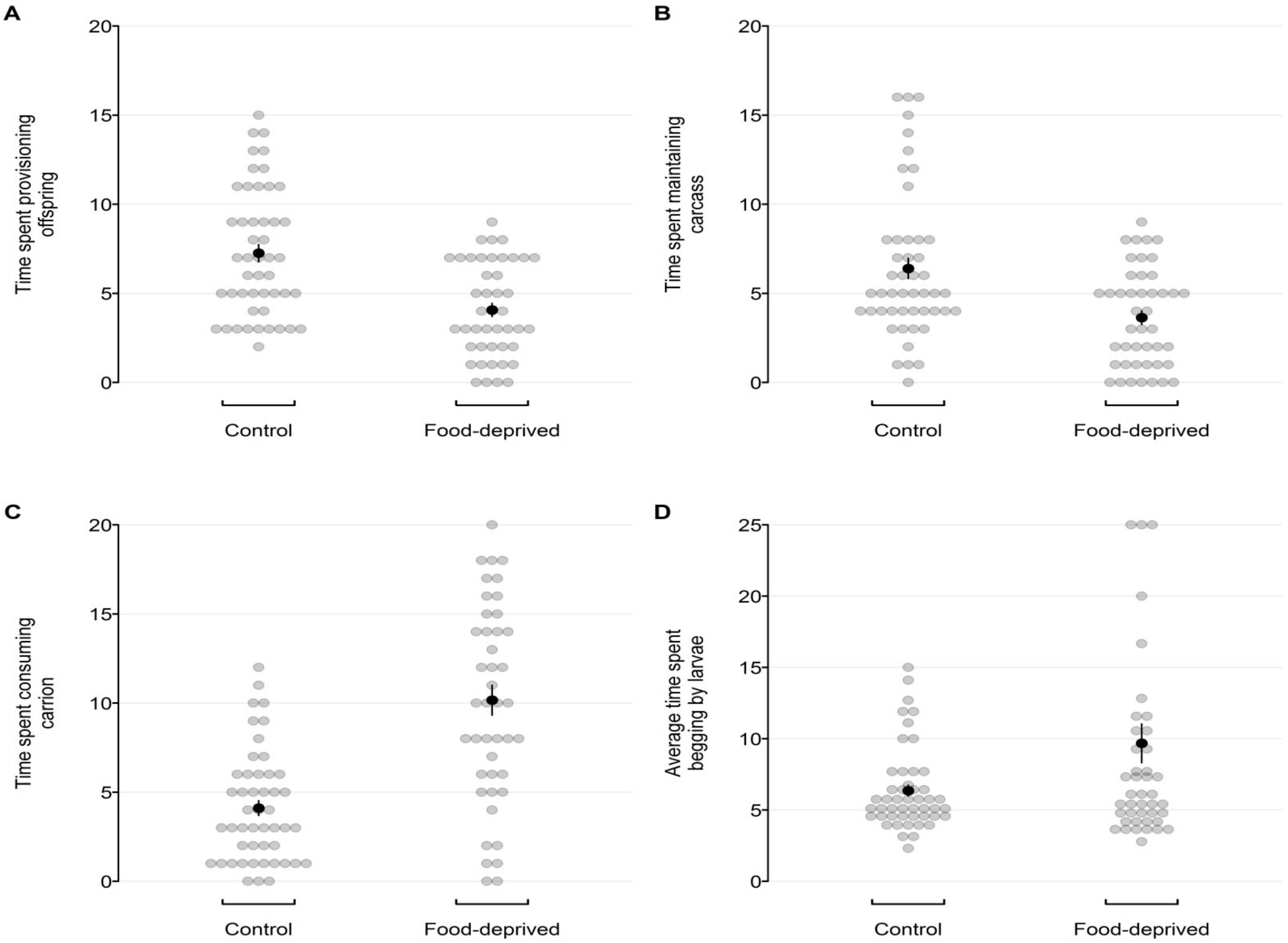
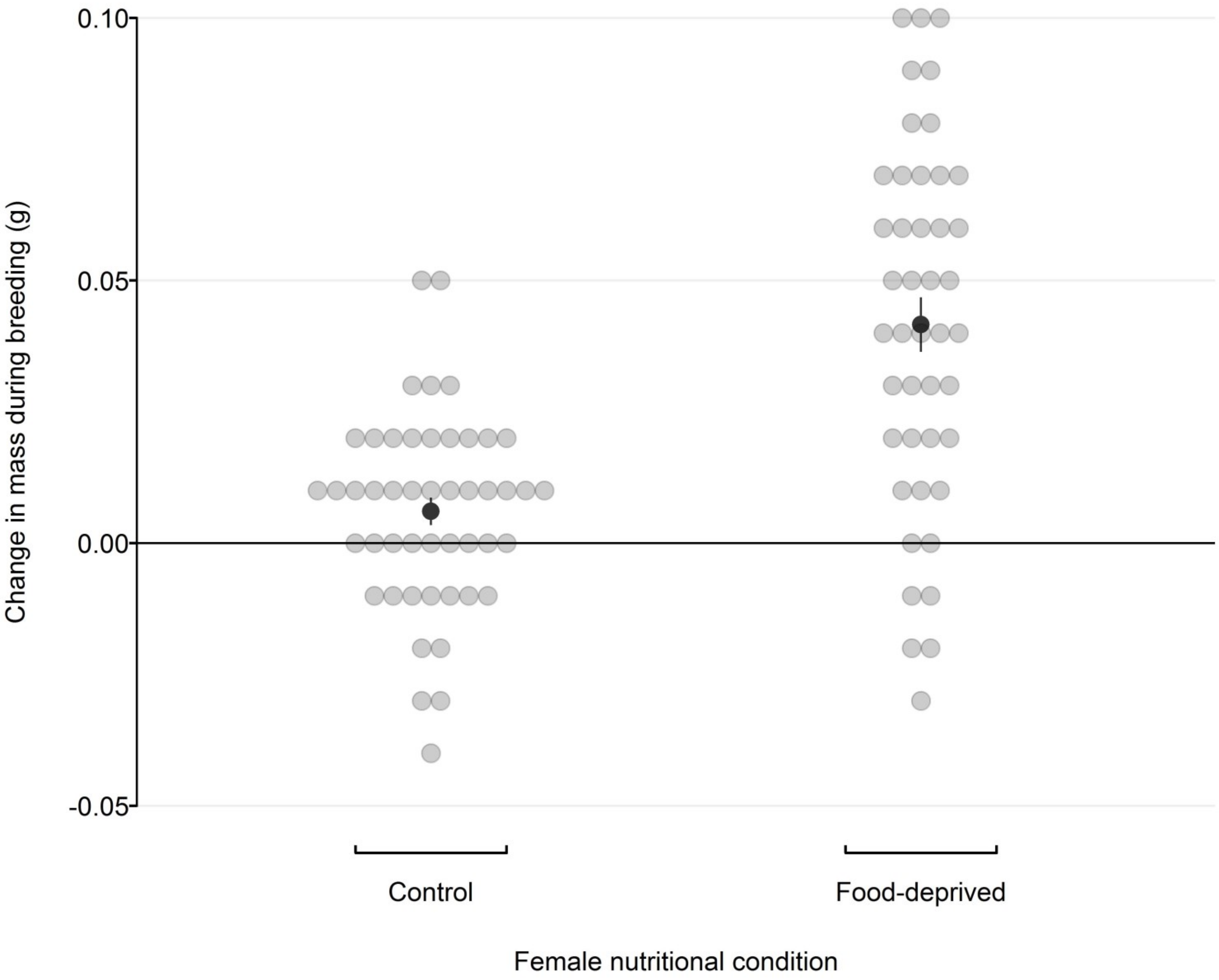
Time until first egg (hours)
Control
Food-deprived
Female nutritional condition


A
Time spent provisioning offspring
20
15
10
5
0
Control
Food-deprived
B
Time spent maintaining carcass
20
15
10
5
0
Control
Food-deprived
C
Time spent consuming carrion
20
15
10
5
0
Control
Food-deprived
D
Average time spent begging by larvae
25
20
15
10
5
0
Control
Food-deprived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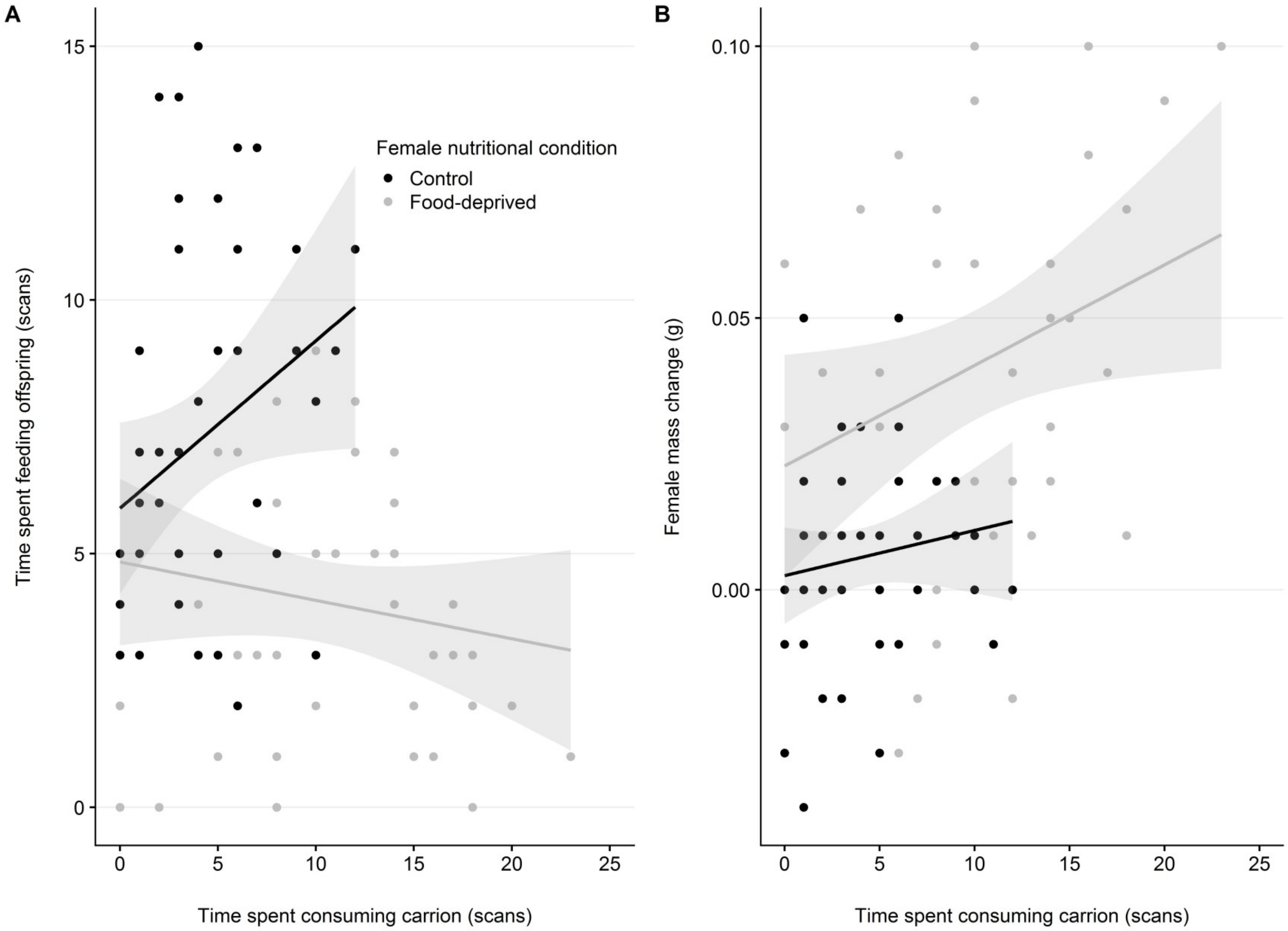
0.05
0.00
-0.05
Change in mass during breeding (g)
Control
Food-deprived
Female nutritional condition

558


A
Time spent feeding offspring (scans)
15
10
5
0
Time spent consuming carrion (scans)
0
5
10
15
20
25
Female nutritional condition
● Control
● Food-deprived
B
Female mass change (g)
0.10
0.05
0.00
Time spent consuming carrion (scans)
0
5
10
15
20
25