Standard metabolic rate is associated with gestation duration, but not clutch size, in speckled cockroaches *Nauphoeta cinerea*

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Summary

Metabolic rate varies significantly between individuals, and these differences persist even when the wide range of biotic and abiotic factors that influence metabolism are accounted for. It is important to understand the life history implications of variation in metabolic rate, but they remain poorly characterised despite a growing body of work examining relationships between metabolism and a range of traits. In the present study we used laboratory-bred families (one sire to three dams) of *Nauphoeta cinerea* (Olivier) (speckled cockroaches) to examine the relationship between standard metabolic rate (SMR) and reproductive performance (number of offspring and gestation duration). We show that SMR is negatively associated with female gestation duration. Age at mating is negatively associated with gestation duration for females, and mass is negatively associated with the average gestation duration of the females a male was mated with. In addition to the results in the current literature, the results from the present study suggest that the association between metabolism and life history is more complex than simple relationships between metabolism and various fitness traits. Future work should consider longitudinal, ontogenetic as well as selective and quantitative genetic breeding approaches to fully examine the associations between metabolism and fitness.

Introduction

Metabolic rate varies widely over a broad range of species, but also varies considerably within a single species (McNab, 2002; Speakman et al., 2004; Steyermark et al., 2005; Millidine et al., 2009; Burton et al., 2011). It has been demonstrated that metabolism is affected by various biotic and abiotic factors including mass, age, sex, activity level, behaviour, reproductive and absorptive states as well as temperature, thermoregulatory strategy and aridity (McNab, 1997; Mueller and Diamond, 2001; Addo-Bediako et al., 2002; White et al., 2007; Careau et al., 2009; Sadowska et al., 2009; Careau et al., 2010; Careau et al., 2011; White and Kearney, 2012). Mass is known to account for the majority (>90%) of the interspecific variation in metabolic rate (Mueller and Diamond, 2001; White et al., 2006; Chown et al., 2007; McNab, 2008), but the metabolic rate of individuals from similarly-sized species of ectotherms can differ by over an order of magnitude. A two–five-fold difference in metabolic rate can exist even among individuals of the same species (Speakman et al., 2004; Steyermark et al., 2005; Millidine et al., 2009; Schimpf et al., 2012). Although the field of study on the life-history implications of such variation has been gaining momentum over the last decade, the fitness consequences of such large inter-individual variation in metabolic rate are not thoroughly characterised (Burton et al., 2011).

It has been suggested the variation between individuals in metabolism may arise as a result of natural selection acting on various life history traits that are correlated with metabolic rate. Thus there may be fitness consequences associated with relatively high or low metabolic rates, yet the strength and direction of the relationship between metabolism and various proxies for fitness is not consistent (Burton et al., 2011). A negative relationship with metabolic rate exists for juvenile *Helix aspersa* (garden snail) survival, over-winter survival in *Tamiasciurus hudsonicus* (North American red squirrels), as well as the survival of food limited *Ulvaria subbifurcata* (radiated shanny), and others (Bochdansky et al., 2005; Cano and Nicieza, 2006; Artacho and Nespolo, 2009b; Larivée et al., 2010). Conversely, metabolic rate is positively correlated with food processing in juvenile *Salmo salar* (Atlantic salmon) and over-winter survival in *Microtus agrestis* (short-tailed field voles) (Jackson et al., 2001; Millidine et al., 2009). Additionally, several studies have revealed no link between metabolic rate and survival in *Myodes glareolus* (bank voles) and *Nauphoeta cinerea* (speckled cockroaches) (Boratyński and Koteja, 2009; Schimpf et al., 2012), or other traits (Hayes et al., 1992; Chappell et al., 1999; Johnson et al., 2001; Nespolo et al., 2005; Bacigalupe et al., 2010; Bouwhuis et al., 2011; Timonin et al., 2011).

The ultimate measure of fitness (lifetime reproductive success) comprises both survival and reproduction. Several studies to date have examined survival under various conditions, and others have looked at measurements of reproductive success. Lifetime reproductive success is logistically very difficult to measure for the majority of taxa (Clutton-Brock, 1988), and, therefore measurement of discrete components of reproductive performance is common practice in this area of research. Blackmer and colleagues, for example, demonstrated that male *Oceanodroma leucorhoa* (Leach's storm petrels) with relatively low metabolic rates had earlier egg-hatching times and higher rates of chick-wing growth than males with higher metabolic rates (Blackmer et al., 2005). In *Myodes glareolus* metabolic rate was positively correlated with overall reproductive success (number of offspring) (Boratyński and Koteja, 2010). On the other hand, no correlation exists between metabolic rate and reproductive performance in *Mus musculus* (mice) or *Sigmodon hispidus* (cotton rats) (Derting and McClure, 1989; Hayes et al., 1992; Duarte et al., 2010). Most of these studies have focused on endothermic vertebrates, and comparatively little attention has been given to ectotherms.

In the present study we add to the growing body of literature that examines the consequences of variation metabolism between individuals by testing for correlations between standard metabolic rate (SMR) and reproductive performance in an insect, *Nauphoeta cinerea* (the speckled cockroach). SMR represents the minimum rate of energy turnover required for life to be sustained (Speakman et al., 2004) and is measured as the metabolic rate of a resting, non-growing, non-reproductive and post-absorptive individual (McNab, 1997; Frappell and Butler, 2004; Hulbert and Else, 2004; Norin and Malte, 2011). SMR is repeatable over short timescales (24 h) in *N. cinerea* (intraclass correlation coefficient $r=0.63$, 95% CI: 0.31–0.68), but its repeatability declines over longer timescales on the order of several weeks (mean time between measurements 39.8 days, range 37–52 days, $r=0.06$, 95% CI: -0.31 to 0.41) (Schimpf et al., 2012). In the present study, we give measures of two aspects of reproductive performance (number of offspring and gestation duration) and report associations between reproductive performance and the SMR of both males and females. By testing for associations between SMR and reproductive performance in a laboratory setting, the present study eliminates any differences in foraging cost between individuals by standardising food availability and ensures that variation in metabolic rate between individuals do not arise as a consequence of downregulation of metabolism associated with food restriction (e.g. Schimpf et al., 2012; Van Leeuwen et al., 2012). We are also able to control and account for the age at which the cockroaches reproduce, and by using an ectothermic study species that exhibits little maternal and no paternal care (Moore, 1994; Bell et al., 2007) we have limited variation in metabolism that may have arisen from differences in thermoregulatory energy expenditure or parental care.

Materials and Methods
Overview
Speckled cockroaches *Nauphoeta cinerea* (Olivier 1789) were maintained in a breeding stock population originally sourced from the Herp Shop (Ardeer, Victoria, Australia). The stock population was maintained in the laboratory under standard temperature and light conditions (25 ± 1.5°C, 12L:12D photoperiod) and fed fresh carrot and commercial cat food pellets (Coles Supermarkets Australia, Tooronga, Australia) *ad libitum*. All water was obtained via moisture from carrots.

Late instar juveniles (male and female) were selected haphazardly from the stock population and kept individually in 1 L polypropylene containers (Lida Trading Company, Brisbane, Australia) in order to allow for the tracking of individuals. Containers were modified by creating ventilation holes in the sides as well as by painting a strip of non-stick Fluon (The Herp Shop, Ardeer, Victoria, Australia) around the inside of the container to prevent escape when the lid was not in place (during cleaning and feeding). Individually housed cockroaches were maintained under the same temperature and photoperiod conditions as the stock population.

Juvenile cockroaches were monitored daily for individuals that had completed the final moult into adulthood. This was termed the 'birthday' and henceforth any reference to the age of cockroaches in days refers to the time since reaching adulthood. Monitoring for adults was ongoing and resulted in the formation of approximately 50 families, where 50 sires were each mated to three dams (one sire and his three dams were considered one family). The metabolic rate of each cockroach was measured, after which males were sequentially mated to the females in his family.

CO$_2$ emission characterisation
Rate of CO$_2$ emission was used as a proxy for metabolic rate and was measured using standard flow-through respirometry techniques according to the methodology described in (Schimpf et al., 2012). Briefly, cockroaches were placed in 25 mL chambers to which dry (Drierite, Sigma–Aldrich, Steinheim, Germany), CO$_2$-free (Soda Lime, Fluka, Steinheim, Germany) air was delivered at a flow rate of 200 mL min^{-1}. CO$_2$ levels from the chambers were measured using a LI-COR 7000 CO$_2$–H$_2$O analyser (LI-COR, Nebraska, USA) or a LI-COR 820 CO$_2$ analyser (LI-COR, Nebraska, USA) and flow rates were regulated using mass flow controllers (GFC17, Aalborg, Orangeburg, New York, USA). Respirometry measurements lasted between 90 and 120 minutes, with at least the initial 30 minutes allocated as a 'settling in' period. Mean rate of CO$_2$ production was then calculated over a 60-minute period (corresponding to low and stable CO$_2$ production) using the following equation (Withers, 2001):

$$\dot{V}CO_2 = (\dot{V}_i \times F_eCO_2) \div [1 + (\{1 \div RER\} - 1) \times F_eCO_2]$$

where $\dot{V}CO_2$ = rate of CO$_2$ emission, $\dot{V}_i$ = incurrent flow rate, F_eCO_2 = excurrent fraction of CO$_2$ and RER = respiratory exchange ratio which was assumed to be 0.8. Data were visually inspected to ensure that $\dot{V}CO_2$ was low and stable throughout the 60-minute period, and data including increases $\dot{V}CO_2$ attributable to periods of activity were excluded from analysis. It is not possible to record resting metabolic rates over shorter periods in this species, as some individuals exhibit periods of spiracular closure lasting several minutes (Schimpf et al., 2009; Matthews and White, 2011; Schimpf et al., 2012).

Rate of CO$_2$ emission was characterised at 25 ± 1.5°C for the majority of cockroaches on day four. Owing to equipment constraints, occasionally these measurements were carried out on day three or five. Cockroaches were fasted for 36–48 hours prior to measurement in order to ensure a post-absorptive state, and mass was recorded after measurement. Rate of CO$_2$ emission was characterised prior to mating for both females (mean duration between measurement of rate of CO$_2$ emission and mating: 3.1 ± 1.3 [s.d.] d, range 1–6 d) and males (mean duration between measurement of rate of CO$_2$ emission and mating: 4.9 ± 2.2 d, range 1–12 d).

Reproductive performance
Both males and females become sexually mature at 6 days of age (Moore et al., 1995; Moore and Sharma, 2005). Males were mated with each of the three females assigned to his family. Matings were coordinated to occur between day six and 10 for the females (i.e. before a delay in mating resulted in apoptosis of the ova (Moore and Sharma, 2005)), and between day six and 15 for males. Males were introduced to the female container for the duration of the active phase (night). Incidental observations confirmed this was sufficient to induce mating. Males were given a rest period of 24 h between matings to minimise any sperm depletion that may have been associated with subsequent ejaculates. Food was provided during the mating period as normal. Data for the two response variables (gestation duration and clutch size) were then collected by monitoring females daily and recording the time until the arrival of the first clutch and number of juveniles it contained.

Logistical constraints dictated that there were ultimately families with varying numbers of dams (3-dam n=33, 2-dam n=12 and 1-dam n=3). Differences in the number of dams per family were due to reasons such as unexpected death without suitably aged replacement or exclusion. Since we could not be certain whether the absence of a clutch was due to lack of mating or other reasons, females that did not produce offspring were excluded.

Analysis
Analyses were conducted using JMP v.8.0.2 (SAS Institute Inc., Cary, NC, USA) and α was set at 0.05 for all tests. Initial models included all variables and interactions in a full factorial combination. When simplifying models, a backwards stepwise elimination approach was taken and any non-significant (p>0.1) variables or interactions were removed with the caveat that main effects were retained if they appeared in an interaction that was retained. Variance inflation

factors were calculated for all variables to check for collinearity; variance inflation factors were always less than 10.

Females

Multiple mixed effects regression models were used to determine the association between metabolic rate and both number of offspring and gestation duration. Both models also included mass, order and age at mating, as well as male identity as a random effect in order to account for the non-independence of clutches sired by the same male. The data for female gestation were transformed [$\log_{10}$(gestation − (minimum gestation − 1))] to minimise the influence of a few right-skewed data-points, and data for number of offspring were log transformed.

Males

To account for the effect of female variation, both the mean number of offspring and mean gestation duration for females mated to a single male were calculated, and were transformed as for females. Multiple regression models were used to determine the association between average metabolic rate and both mean number of offspring and mean gestation duration for males. In addition to metabolic rate, mass and mean age at mating were included as fixed variables.

Results

Summary statistics for all measured traits are provided in Table 1.

Females

The only variable that remained in the minimum adequate model for number of offspring was age of mating, which had a non-significant negative association with number of offspring (Table 2). The minimum adequate model for gestation duration included both metabolic rate and age, which were both significantly negatively associated with gestation duration (Table 2). Females with a higher metabolic rate had a shorter gestation duration (Fig. 1A), as did older females compared to younger females (Fig. 1B) (age at mating range 6–10 days).

Males

The only variable that remained in the minimum adequate model for the average number of offspring was male mass, which had a non-significant positive association with the number of offspring (Table 2). The minimum adequate model for mean gestation duration included male mass, which was significantly negatively associated mean gestation duration (Table 2). Females mated with heavier males had shorter gestation durations than females mated to lighter males (Fig. 2).

Discussion

The association between female metabolic rate and reproductive output

Number of offspring

There were no associations between the number of offspring a female produced and any of the parameters we measured. We had

Table 1. Summary statistics for body mass, rate of CO_2 production ($\dot{V}CO_2$), gestation duration, and number of offspring per clutch.

	Mean	s.d.
Males (n=48)		
Mass (g)	0.51	0.07
$\dot{V}CO_2$ (ml h^{-1})	0.109	0.012
Females (n=126)		
Mass (g)	0.63	0.09
$\dot{V}CO_2$ (ml h^{-1})	0.133	0.019
Gestation duration (d)	56.4	2.3
Number of offspring	35.4	2.7

anticipated an association between the number of offspring a female produced and her metabolic rate, because of the relatively high maternal investment in this species (Moore and Moore, 2001), and the assumption that individuals with low SMR would be better able to make this investment and would therefore produce more offspring (the compensation hypothesis) (Nilsson, 2002; Blackmer et al., 2005; Boratyński and Koteja, 2010). This investment consists not only of the high energetic costs of producing gametes and provisioning them with nutrients (Hayward and Gillooly, 2011), but also incorporates the cost of carrying the developing young (although this species is ovoviviparous and no nutrients are passed to the developing embryos, the females must still carry the young in the brood pouch until they emerge (Moore and Moore, 2001; Moore and Sharma, 2005; Bell et al., 2007). Females also provide some parental care by protecting the young immediately after emergence (Moore and Moore, 2001; Bell et al., 2007; personal observation). An alternative to the compensation hypothesis is the increased-intake hypothesis, which predicts that animals with a relatively high SMR should be able to absorb and process more energy than those with relatively low SMR, and should therefore be able to devote more energy to reproduction attain superior reproductive success (Nilsson, 2002; Blackmer et al., 2005; Boratyński and Koteja, 2010). A third alternative is that high SMR is associated with both high self-maintenance costs and high capacities for energy uptake, thereby obscuring any relationship between SMR and reproductive performance.

Age also did not affect the number of offspring produced by a female, which is in contrast to other studies on the same species that found that older females produce fewer offspring (Moore and Harris, 2003). Our study, however, differs from that of Moore and Harris in that their 'older' females were 18 days old (Moore and Harris, 2003) as opposed to our 'older' females that were only 10 days old. It is likely the processes that underlie a decrease in reproductive output (e.g. oocyte apoptosis) (Moore and Sharma, 2005) associated with age are not sufficiently progressed by 10 days for a correlation to be revealed. Indeed Moore and Moore also found no decrease in reproductive output by 10 days of age, despite an increase in oocyte apoptosis for the same time period (Moore and Moore, 2001).

Gestation duration

Both metabolic rate and age were negatively associated with the gestation duration, as has previously been demonstrated in comparative analyses of mammals (McNab, 1980; Symonds, 1999). Females with a relatively high metabolic rate prior to mating displayed a shorter gestation duration, which may be beneficial for females, if a shorter gestation enhances fitness by reducing the time a female needs to bear the cost of carrying her young, and by increasing the number of clutches a female can potentially produce during her life. It has been suggested that faster developing offspring may trigger earlier parturition (Bourdon and Brinks, 1982), which could explain the negative association between metabolism and gestation duration in this species, if females with a higher metabolic rate produce faster developing offspring. This idea is supported by the positive genetic association between metabolic rate and post-weaning growth rate in voles (Sadowska et al., 2009). However, in *Oceanodroma leucorhoa* (Leach's storm petrels), males with a relatively low metabolic rate have been shown to produce chicks

Table 2. Parameter estimates and significance tests for the putative correlates of reproductive performance in *Nauphoeta cinerea*. Predictors indicated with * were retained in the minimum adequate model; all other predictors were removed during stepwise backwards elimination. Mass is in g, ages and durations are in days (transformed as described in the text), $\dot{V}CO_2$ is in ml min^{-1}.

Term	Estimate	t_{df}	p
Response: $\log_{10}$(number of babies)			
Female mass	-0.053 ± 0.048	$t_{121} = -1.11$	0.27
Female $\dot{V}CO_2$	10 ± 10	$t_{121} = 1.01$	0.32
Mating order	0.007 ± 0.004	$t_{97} = 1.6$	0.11
Intercept*	1.58 ± 0.02	$t_{112} = 84.0$	< 0.0001
Female age at mating*	-0.0047 ± 0.0026	$t_{108} = -1.82$	0.07
Male variance component*	0.00019 ± 0.00013		
Response: $\log_{10}$(gestation duration)			
Mating order	-0.004 ± 0.023	$t_{95} = -0.19$	0.85
Female mass	0.19 ± 0.26	$t_{122} = 0.74$	0.46
Intercept*	1.41 ± 0.15	$t_{116} = 9.34$	< 0.0001
Female $\dot{V}CO_2$ *	-135 ± 54	$t_{123} = -2.49$	0.01
Female age at mating*	-0.072 ± 0.014	$t_{106} = -5.16$	< 0.0001
Male variance component*	0.007 ± 0.004		
Response: $\log_{10}$(number of babies)			
Male $\dot{V}CO_2$	-2.39 ± 17.0	$t_{43} = -0.14$	0.89
Mean male age at mating	0.001 ± 0.003	$t_{44} = 0.21$	0.83
Intercept*	1.51 ± 0.02	$t_{46} = 62.8$	< 0.0001
Male mass*	0.09 ± 0.05	$t_{46} = 1.82$	0.08
Response: $\log_{10}$(gestation duration)			
Mean male age at mating	-0.01 ± 0.02	$t_{43} = -0.63$	0.53
Male $\dot{V}CO_2$	-143 ± 142	$t_{45} = -1.01$	0.32
Intercept*	1.01 ± 0.21	$t_{46} = 4.72$	< 0.0001
Male mass*	-1.05 ± 0.42	$t_{46} = -2.5$	0.02

with a faster wing-growth rate than males with relatively high metabolic rates (Blackmer et al., 2005).

Age was also negatively associated with gestation duration such that older females at mating showed shorter gestation duration. This finding is in contrast with a wide range of studies on mammals (e.g. cattle, pigs, hamsters) that found either no association between gestation duration and age (reviewed by Andersen and Plum, 1965; see also Omtvedt et al., 1965; Reynolds et al., 1980) or a positive association (reviewed by Soderwall et al., 1960; Andersen and Plum, 1965; Bourdon and Brinks, 1982; Echternkamp and Gregory, 1999). For *N. cinerea* Moore and Moore report that older mothers take longer to produce a clutch (Moore and Moore, 2001), but this relationship only appears after ~10 days of age (i.e. after the 'old' age of our females, as discussed earlier). Prior to this, however, gestation duration remains constant (Moore and Moore, 2001), so the reason why gestation duration declined with age in the present study is unclear. Perhaps egg quality (e.g. size, energy content) continues to increase over this period such that young develop faster, until egg quality decreases after 10 days. To determine if this is the case, further examination of egg quality over the first weeks of adulthood is required.

The association between male metabolic rate and reproductive output
#### Number of offspring
Interestingly, none of the male variables (metabolic rate, mass or age) were significantly associated with the mean number of offspring he produced across the matings within his family. Although sperm are generally considered energetically inexpensive, especially compared to reproductive costs for females (e.g. Dewsbury, 1982; Hayward and Gillooly, 2011), the energetic cost of reproduction for males (number, size and mobility of sperm as well as associated fluid) is nonetheless significant (Dewsbury, 1982; Harris and Moore, 2005; Hayward and Gillooly, 2011). It is therefore plausible to expect some kind of association with metabolism. Indeed ejaculate production is usually traded off against other demands including growth, maintenance, mate finding, immunity and lifespan (Dewsbury, 1982; Van Voorhies, 1992; Sella and Lorenzi, 2003; Simmons and Roberts, 2005). We expected that males with lower self-maintenance costs could potentially produce more or 'better quality' sperm and accordingly achieve increased reproductive output, but this idea receives no support from the present study. We note, however, that the present study was not designed to test for an association between metabolic rate and sperm quality, and future work measuring sperm quality directly would provide a more robust test for such an association.
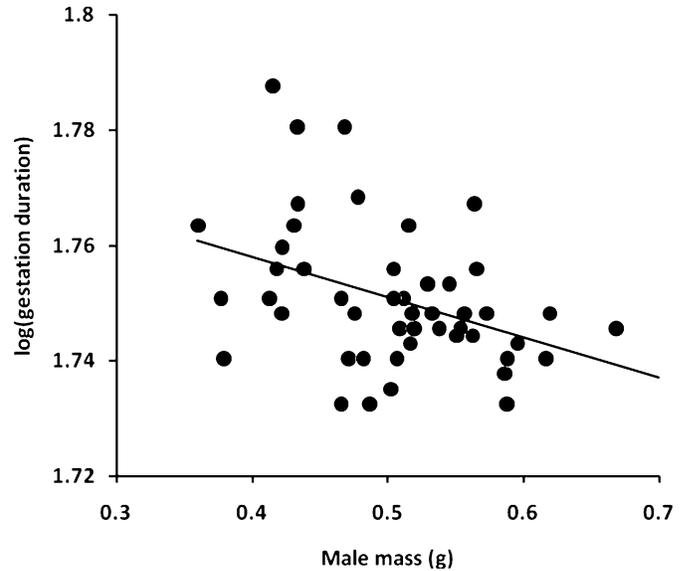
Gestation duration
Mass was significantly associated with the mean gestation duration of the females that males were mated to, and on average, females mated to heavy males had the shortest gestation durations. Of the associations revealed by the present study, this is possibly the most difficult relationship to explain, especially when trying to rationalise the mechanisms by which male mass is associated with gestation duration. Female mass was not associated with gestation, which makes the association for males all the more curious, since males provide only a relatively small contribution to reproduction (sperm). The association certainly does not arise as a consequence of the positive association between metabolic rate and body mass, as there was no relationship between the metabolic rate of males and the gestation duration of females to which they had been mated. It is also unlikely that the mechanism is via partner care (e.g. food provisioning or protection) since this is not provided.

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A

B
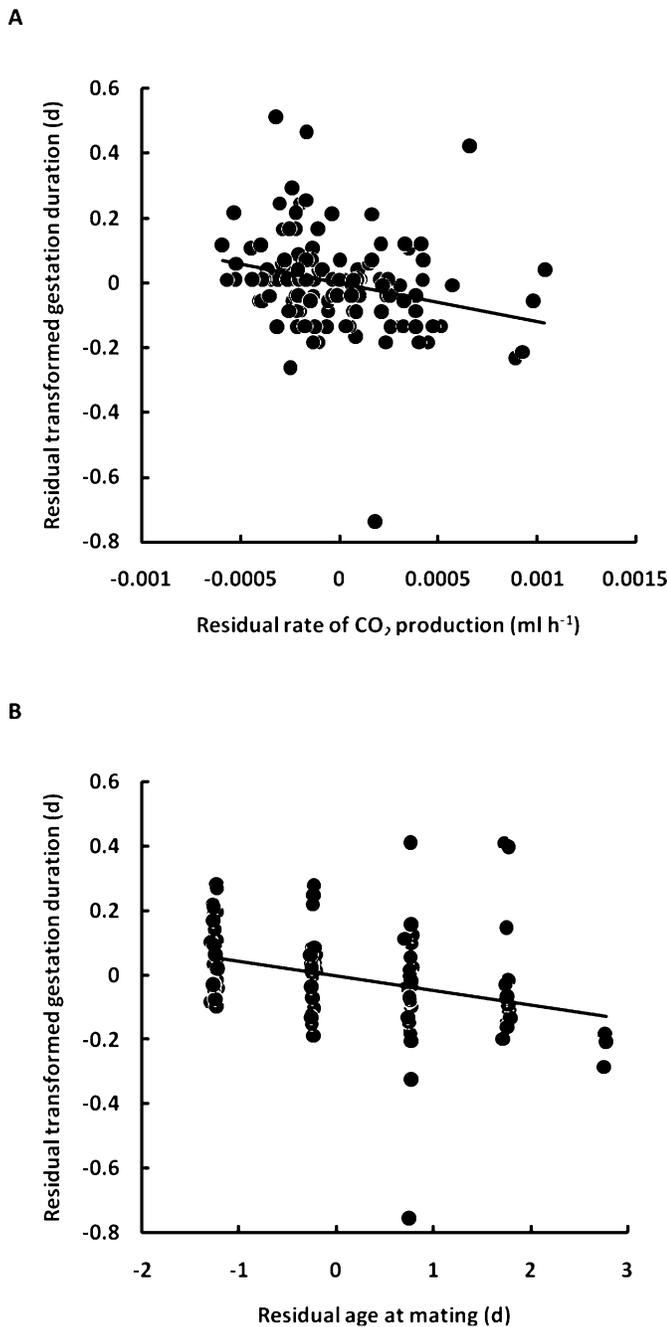
Fig. 1. (**A**) The relationship between residual rate of CO_2 production (metabolic rate) and residual transformed gestation duration and (**B**) between residual age and residual transformed gestation duration for female *Nauphoeta cinerea* (n=126). Females with a higher metabolic rate have a shorter gestation duration, as do females that were relatively older at mating. Gestation duration transformation = $\log_{10}$(gestation − (minimum gestation − 1)). The low gestation duration outlier had no leverage on the relationship.

There is much evidence to indicate that males of some species manipulate their mates, often to the detriment of the females (Lew and Rice, 2005). In *Drosophila melanogaster*, for example, the behaviour and seminal fluids of males affects the survival, fecundity or fertility of females (Fowler and Partridge, 1989; Chapman et al., 1995; Rice, 1996; Moore et al., 2001; Pitnick and García-González, 2002). In *N. cinerea*, females' assessment of

Fig. 2. The relationship between male *Nauphoeta cinerea* (n=48) mass and the average gestation duration of the females he was mated with. Females mated with heavier males had a shorter average gestation duration than those mated with lighter males.

male pheromone constitutes the males' attractiveness (Moore, 1988; Moore, 1994; Moore et al., 2001). Male attractiveness is genetically correlated with the rate at which his offspring develop, with attractive males producing faster developing offspring (Moore, 1994) and thereby influencing the time between matings (Moore et al., 2001). Thus, assuming that male pheromone underlies the correlation between male attractiveness and offspring development, and that larger males produce more or more attractive pheromones, it is possible that associations between mass and pheromone production underlie the association between male mass and female average gestation observed in the present study. Such an association would be augmented if there is a genetic link between male size and rate of offspring development (such that larger males produce faster-developing offspring), but the breeding design in the present study is not sufficient to determine if this is the case.

Additionally, many species of cockroach provide nuptial gifts in the form of tergal secretions (Bell et al., 2007). The secretions are phagostimulants upon which females feed during courtship and initial mating (Bell et al., 2007; Mondet et al., 2008). If the provisioning of secretions enhances reproductive performance, and if large males provide more or higher quality secretions than small males, then possibly female gestation is influenced in this way. A study of *Leucophaea maderae* (the Madeira cockroach) showed that these tergal secretions did not translate to increased reproductive success in the females (Mondet et al., 2008), but it is not clear if this observation extends to gestation duration.

Conclusions

It is clear from the results of the present study that there is no consistent association between reproductive performance and metabolic rate for male and female *N. cinerea*. It is also possible that more associations with metabolic rate were not revealed due to the fact that the long-term repeatability of metabolic rate is low in this species (Schimpf et al., 2012). In a previous study, we

demonstrated short term (one day) but not longer term (five weeks) repeatability of metabolic rate in male speckled cockroaches (we are yet to examine repeatability in females) (Schimpf et al., 2012). Despite this, however, a correlation between reproductive performance and metabolic rate was nonetheless revealed in the present study. Perhaps the short term repeatability is sufficient to produce an effect as we have previously surmised (Schimpf et al., 2012). Then again, only one association with metabolic rate was revealed and the fact that no further associations were revealed could in fact be due to the decline in repeatability of metabolic rate over time.

Suggestions have been made that metabolic rate is a repeatable measure over time (Marais and Chown, 2003; Nespolo et al., 2003; Labocha et al., 2004; Rønning et al., 2005; Nespolo and Franco, 2007; Szafrańska et al., 2007; Lardies et al., 2008; Artacho and Nespolo, 2009a; González et al., 2010; Larivée et al., 2010; Maciak and Konarzewski, 2010), but other studies have found a decrease in the repeatability of metabolic rate in the long term (Vézina and Williams, 2005; González et al., 2010; Larivée et al., 2010; Bouwhuis et al., 2011; Norin and Malte, 2011), and others have shown low or non-significant repeatability even in the short term (Bozinovic, 2007; Russell and Chappell, 2007). Despite this apparent decline in repeatability of metabolic rate in some species, it remains that metabolic rate is correlated with a measure of reproductive performance in the present study. On the other hand, multiple studies on several species (e.g. mice, bank and meadow voles, great tits) has failed to reveal phenotypic correlations between metabolic rate and a range of other traits (Derting and McClure, 1989; Hayes et al., 1992; Chappell et al., 1999; Johnson et al., 2001; Nespolo et al., 2005; Boratyński and Koteja, 2009; Duarte et al., 2010; Bouwhuis et al., 2011; Timonin et al., 2011). It seems that these mixed results from phenotypic correlation tests combined with the fact that metabolic rate is far from universally repeatable suggests that perhaps metabolic rate does not have as great an influence on life history and fitness traits as the current theoretical mindset would have us believe.

Several recent studies, however, suggest that such a view should be adopted cautiously. Firstly, in their quantitative genetic study of *Myodes glareolus* (bank voles), Sadowska and colleagues demonstrated that traits can show additive genetic correlations with metabolic rate that are not necessarily revealed by phenotypic analyses (Sadowska et al., 2009) such as the present study (see also Careau et al., 2011). Secondly, the recently proposed 'context dependence' hypothesis of metabolic rate posits that the relationship between metabolism and fitness may depend on the quality of the environmental conditions an organism inhabits (Burton et al., 2011). These studies highlight the importance of research incorporating longitudinal studies, ontogenetic manipulation of metabolism, selective breeding for different levels of metabolism, and quantitative genetic breeding designs to help understand the relationship between metabolism and fitness. It is clear that the relationship between metabolism and fitness may not be as straightforward as has been assumed in the past and it is important that future research in this area reflects this idea.

Acknowledgements

Competing Interests
The authors have no competing interests to declare.

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