acta ethol (2013) 16:163–172
DOI 10.1007/s10211-013-0147-3

ORIGINAL PAPER

# Predation selects for low resting metabolic rate and consistent individual differences in anti-predator behavior in a beetle

**Indrikis Krams · Inese Kivleniece · Aare Kuusik ·
Tatjana Krama · Todd M. Freeberg · Raivo Mänd ·
Jolanta Vrublevska · Markus J. Rantala · Marika Mänd**

Received: 26 November 2012 / Revised: 19 March 2013 / Accepted: 11 April 2013 / Published online: 30 April 2013

**Abstract** Significant between-individual variation in resting metabolic rate (RMR) of animals is a widespread phenomenon that may have important implications for our understanding of variation in behavior and animal personality. By using wild caught mealworm beetles, *Tenebrio molitor*, we examined the relationships among survival rate under predator tests, individual response latency time to become immobile under the risk of predation, duration of immobility time, and RMR. Individuals with higher levels of RMR were bold, and bold individuals were found to be more exposed to the risk of bird predation. We found that RMR was positively correlated with the latency of immobility response and negatively correlated with the total duration of immobility. The correlation between behavioral responses suggests a behavioral syndrome in the anti-predator behavior of *T. molitor*. The results indicate that energy metabolism may be part of a syndrome that involves behavior and life history traits in animals.

**Keywords** Personality · Behavioral syndrome · Predation · *Tenebrio molitor* · Natural selection

## Introduction

Anti-predator behavior is an important determinant of fitness in many animal species (Godin 1997; Ruxton et al. 2004). The existing evidence shows that animals can adjust their reproductive effort (Godin 1995; Candolin 1998) and their foraging effort to the risk of predation (Lima and Dill 1990; Magnhagen 1990; Ylonen 1994). Trade-offs between reproductive investment and predation risk and between starvation and predation risk are central to many decisions individuals make regarding habitat choice (Gilliam and Fraser 1987; Butler et al. 2005), foraging and mating, and diurnal activity (Dall and Witter 1998; Krause and Ruxton 2002; Macleod et al. 2005; Hedrick and Kortet 2006; Luttbeg and Sih 2010).

Differences among prey individuals in responses either to the mere presence of a predator or to real attacks by the predator are typically viewed as adaptive. Anti-predator responses do not represent just some variation around a mean value but reveal genuine differences in behavioral strategies (Dall et al. 2004; Dingemanse and Réale 2005; Bell and Sih 2007; Réale et al. 2007, 2010; Smith and Blumstein 2008, 2010; Bell et al. 2009; Dingemanse and Wolf 2010). In many species, individual differences in behavior and physiology are consistent across contexts and are stable over time. Such consistent individual differences are referred to as temperament or personality (van Oers et al. 2004; Groothuis and Carere 2005; Sih and Bell 2008; Bell et al. 2009; Dingemanse and Wolf 2010; Gyuris et al. 2011), and

I. Krams (✉) · I. Kivleniece · T. Krama · J. Vrublevska
Institute of Systematic Biology, University of Daugavpils, 5401, Daugavpils, Latvia
e-mail: indrikis.krams@ut.ee

A. Kuusik · M. Mänd
Department of Plant Protection, Institute of Agricultural and Environmental Sciences, Estonian University of Life Science, 51014, Tartu, Estonia

T. M. Freeberg
Department of Psychology and Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TX, USA

I. Krams · R. Mänd
Institute of Ecology and Earth Sciences, University of Tartu, 51014, Tartu, Estonia

M. J. Rantala
Section of Ecology, Department of Biology, University of Turku, 20024, Turku, Finland

behavioral correlations that arise as a consequence of individual variation in two or more behaviors are termed behavioral syndromes. Predation has been proposed as one of the most important mechanisms underlying the maintenance of behavioral syndromes by selecting against certain combinations of traits (Stamps 2007; Luttbeg and Sih 2010). However, there are few studies investigating the relationship between personality traits and anti-predator behavior (Quinn and Cresswell 2005; Bell and Sih 2007; Kortet and Hedrick 2007; Réale et al. 2007; Hollander et al. 2008; Jones and Godin 2010; Kortet et al. 2010; Smith and Blumstein 2010), most likely because predation events are infrequently observed in nature compared with other behavioral phenomena.

Careau et al. (2008) proposed a “performance model” to explain the proximate mechanisms that underlie consistent individual differences in behavior. It was suggested that consistent individual differences in energy metabolism, as reflected by resting metabolic rate (RMR), may be correlated positively with individual differences in metabolically costly anti-predator responses (Biro and Stamps 2010). Several studies have shown relationships between RMR and total energy output in animals (Daan et al. 1990; Hammond and Wunder 1995; Hammond et al. 1996; Hammond and Diamond 1997; Niewiarowski et al. 2000). Although empirical studies of the relationships between resting metabolic rates and total energy output across individuals of the same age, sex, and reproductive state are quite rare (Earle and Lavigne 1990; Hayes et al. 1992; McLean and Speakman 2000; Mueller and Diamond 2001; Zera and Zhao 2006; Castañeda et al. 2010), most of them report positive correlations between resting metabolic rate and sustained energy output (Speakman et al. 2003, 2004; Rezende et al. 2005, 2009; Nespolo et al. 2008).

In this experimental study, we tested whether survival of yellow mealworm beetles exposed to the great tit, *Parus major*, a diurnal predator, is related to their anti-predatory responses, and whether anti-predator behavior can be related to RMR. It has been recently shown that more aggressive males of the field cricket, *Gryllus integer*, have shorter latencies to emerge from safe refuge, are more active in general, and are less cautious towards predation risk compared to less aggressive male crickets (Hedrick and Kortet 2006; Kortet and Hedrick 2007; Niemelä et al. 2012, 2013). To study anti-predator responses, we investigated behavioral variation among yellow mealworm beetles, *Tenebrio molitor*, in their individual response latency time to become immobile and the duration of immobility to treatments mimicking an approach of predator. To assess the role of metabolism, we measured the RMR of each individual beetle and also tested whether RMR was consistently repeatable across individuals, as well as relationships among RMR, survival, and anti-predator responses (Nespolo and Franco 2007). Although yellow mealworms are a popular study object in evolutionary biology (e.g., Moret 2006; Sadd et al. 2006; Vainikka et al. 2006; Kivleniece et al. 2010; Daukste et al. 2012; Krams et al. 2013a, b), repeatabilities in mealworm anti-predator responses and RMR have not been studied so far. It is important to note that repeatability can be considered as the approximate estimate of the upper limit of heritability (Lynch and Walsh 1998; Dohm 2002). When repeatability is low, the measured trait is unlikely to respond to any kind of selection, and it is also unlikely to correlate with the measurements of other traits (Hõrak et al. 2002; Szafranska et al. 2007; Bell et al. 2009).

## Materials and methods

### Beetles

The progenitors of the beetles used in the experiment originated from a natural population. More than 700 beetles were collected from 12 barns in southeastern Latvia in 2007–2010. The stock culture was maintained at Daugavpils University on bran mixed with wheat flour, fresh carrots, and apples in a controlled environment (at 24±2 °C) on a 14:10-h L/D photoperiod. We removed pupae from the culture on the day of pupation, weighed them, and determined their sex by examining the genitalia on the eighth abdominal segment (Bhattacharya et al. 1970). We then kept the pupae and newly emerged adults individually in numbered 200-ml plastic containers filled with a mixture of bran and wheat flour and with fresh carrot/apple pieces offered ad libitum at least twice a week. We excluded all individuals with visible abnormalities from the experiment. All of the experimental trials were conducted in December 2009 and January 2010 at 23 °C. Beetles were weighed to the nearest 0.001 g with an electronic balance (RADWAG 26–600 Radom, Poland), and this measure was highly repeatable between two subsequent days ($r$=0.98, $N$=300, $P$<0.0001). The beetles used in this study were of similar body weight, varying between 0.95 and 1.05 g.

### Flow-through $CO_2$ respirometry to measure RMR

The LI-7000 differential $CO_2$/$H_2O$ analyzer (LiCor, Lincoln, NE, USA) was calibrated at different flow rates by means of calibration gases (Trägergase, VEB, Saxon Junkalor GmbH, Dessau) (Quinlan and Lighton 1999; Lighton 2008) with gas injection (see also Mänd et al. 2005, 2006; Muljar et al. 2012). The insect chamber (Eppendorf test tube, volume 3 ml) was perfused with dry (5–7 % RH) $CO_2$-free air, produced by passing air over Drierite (W. A. Hammond Drierite Co. Ltd, Xenia, OH, USA) and soda–lime granules at a flow rate of 60 ml min$^{-1}$. Baseline drift of the analyzer was corrected during analysis from the measurements at the beginning and end of each trial, with the respirometer chamber empty (Gray and Bradley 2006; Duncan 2003; Duncan and Byrne 2005).

The first measure of RMR was collected when the beetles were 15 days old. Each beetle was kept in the insect chambers until it became motionless and reached the lowest rates of $CO_2$ production. We then waited for an additional 10–15 min and then began recording RMR for 20 min. The mean metabolic rate of each individual was calculated by averaging data obtained over the final 20-min period for each beetle (e.g., Tartes et al. 1999). Since the beetles were either immobile or active just for short periods, the lowest values of recorded $CO_2$ emissions roughly corresponded to the resting metabolic rate of each insect. As soon as the measurements were over, we returned the beetles to their plastic containers.

The RMR trials were repeated 6 days later (age=21 days). Nespolo and Franco (2007) showed that repeatabilities are linearly reduced with time between measurements, suggesting habituation to experimental manipulations. However, the time interval of 6 days seems to be sufficient to avoid habituation in the case of such short-lived organisms as mealworm beetles. The life span of *T. molitor* usually reaches 4 months in our laboratory (Daukste et al. 2012; Krams et al. 2013a, b).

## Imitation of predator approach

There is a wide variety of experimental methods to measure anti-predatory behaviors (here, latency time to become immobile and time spent immobile) in response to imitated predator approach. Many insects, especially beetles, respond to a variety of mechanical or optical stimuli by abruptly reaching a state of more or less complete tonic immobility lasting from a few seconds to several hours. The true tonic immobility in beetles usually is characterized by the lack of regular pumping movements involving both abdominal and thoracic segments, while abdominal movements may be present during freezing behavior (Metspalu et al. 2002). When predators attack, mealworm beetles often feign death by entering a state of tonic immobility. In our studies, as soon as insects reached the age of 25 days, we handled individual beetles for 2 min and then gave them the opportunity to escape into a conical Eppendorf test tube (1.5 ml), which was used as insect chamber. In this tube, the beetles either became less active or completely immobile, as if they were hiding in a dark and safe crevice, whereas they never adopted an immobile pose during handling. The insect chamber was combined with an infrared optical–actographic system using IR-emitting diodes (TSA6203) and IR-sensor diodes (BP104), which were placed on the sides of the insect chamber. The light from the IR-diode was modulated by the abdominal contractions, leg and body movements, and heart activity, and we could discriminate among these activities because the level of the output voltage reflected the vigor of the muscular contractions of the insect (see Hetz (1994); Mänd et al. 2005; Karise et al. 2010). Thus, we could detect whether the beetle was immobile or active. The beetles were left in the insect chamber, and we waited until they became active again as indicated by movements of legs, head, and antennae. When beetles just resumed locomotion by moving the legs, head, and antennae, we exposed them to a sudden and brief mechanical stimulus by flicking the tube from above with a stick to apply a mass of about 20 g dropped from a height of 10 cm. This mimicked a light jump of a landing great tit (*P. major*) onto the insect chamber. We recorded individual response latency time to the mechanical stimulus (time to become immobile) and the time beetles spent immobile. We repeated the trials 5 days later. The repeatabilities of the behavioral responses obtained by I.K. and I.K. were high ($r$=0.97 and 0.982 for response latency time and the time beetles spent immobile; all $P$<0.0001). In total, we obtained behavioral data from 300 individuals (150 males and 150 females).

## Predators and survival experiment

Major predators of wild mealworm beetles living in barns include birds and rodents. Since great tits often visit barns and have been seen attacking mealworms under twilight conditions of barns (Krams et al., numerous personal observations), we used these birds as predators in this study. Fifteen great tits (14 males and one female) were captured a day before the beetle survival trials. Prior to the trials, birds were kept in individual cages with water and food ad libitum. As soon as the trials were over, the birds were immediately released at the place of capture. The longest time a great tit was held in captivity for this study was 18 h.

To provide a measure of the effect of individual anti-predator responses on survival, we placed beetles in bird cages, which served as predation exposure arenas (30×40×40 cm, L×W×H) and exposed them to great tits deprived of food for 2 h before the onset of the trials. The predation trial arena was set up to be as natural as possible, given the constraints of the small enclosure. The floor of each arena was covered with a 2-cm layer of bran, which provided beetles their usual food supply. The bran layer was thick enough to allow the beetles to walk and run without slipping and to burrow out of sight. All of the beetles were individually marked by drawing small dots on the dorsal side of the abdomen with a correction pen. During a preliminary study, the birds consumed the marked beetles in 72 of 145 cases (two-tailed sign-test: $Z$=0.03, $P$=0.98), which shows that markings did not significantly influence the survival of mealworm beetles.

An hour before each predation trial, beetles were released into the predation cage to familiarize themselves with the environment. This gave them ample time to search out and find cover. In each trial, we used ten randomly chosen individuals. We carried out survival experiments separately for male and female mealworm beetles. Before the predator was released into the predation exposure arena, we ensured that no beetles were left lying on their backs. The birds started to attack the beetles within the first minutes of the survival trial. Each predation trial lasted for 15 min. We observed the behavior of birds and beetles from a hide. As soon as the trial was over, we removed the birds and counted the survivors.

Each great tit was used only twice: during the male survival experiment and during the female survival experiment, which were separated by a 1-h break for each individual bird. The order of trials was chosen randomly for each sex of beetles and for each predator. Thus, each individual test beetle with known RMR (see above) was exposed to two predator approach tests in a hide (the insect chamber) and to the survival test.

### Data analysis

To ascertain whether individual test beetles were consistent in their behavior, the repeatabilities (*R*) of response latency time to the mechanical stimulus and the total time beetles spent immobile were calculated across two trials using Lessells and Boag's (1987) method. From both measures, mean values were calculated and used thereafter. The existence of a behavioral syndrome was then assessed from the correlation between response latency to mechanical stimulus and the duration of immobility. Statistical tests were two-tailed and all of the analyses were performed in SPSS 17.0 for Windows (SPSS Inc). All dependent variables were non-normally distributed and subjected to square root transformations to comply with normality assumptions of ANCOVA. Since body weight used as a covariate in ANCOVA analyses did not affect behavioral responses, we removed it from the remaining analyses.

### Ethical note

The great tits were kept for the needs of the behavioral experiment and were released within 2–3 h after the mealworm survival tests at their place of capture. We performed the experiment using live beetles to obtain really valid dependent measures linking RMR to survival, and it was not possible to "model" predation events in this study (Barnard 2007; Cuthill 2007; Fedigan 2010).

## Results

### Consistency of behavior over time

The latency to become immobile in response to flicking the insect chamber varied between 2 and 118 s (26.89±20.34, mean ± SD), and the total time spent motionless after flicking varied between 4 and 920 s (287.03±195.98, mean ± SD). Individuals were significantly repeatable both in the response latency after flicking of the insect chamber ($R$=0.854, $F_{299,300}$=26.304, $P$<0.001) and in the total time spent immobile ($R$=0.593, $F_{299,300}$=13.095, $P$<0.001). The RMR (49.00±40.53 $VCO_2$ μl h$^{-1}$, mean ± SD) likewise was found to be repeatable among individual beetles ($R$=0.574, $F_{299,300}$=16.217, $P$<0.001).

### Determinants of anti-predator behavior

The response latency to flicking and the total time spent immobile were negatively correlated (Pearson's $r$=−0.83, $t_{298}$=−6.204, $P$<0.001; Fig. 1), suggesting that individuals more prone to freezing behavior spent more time motionless under the risk of predation. GLM analysis showed that both the response latency to the mechanical stimulus and the total time spent immobile were dependent on the RMR (a covariate in GLM), while sex and the interaction between sex and the RMR did not affect the behavioral responses under predation risk (Table 1). The response latency to flicking the insect chamber and the RMR were positively correlated (Pearson's $r$=0.489, $t_{298}$=4.517, $P$<0.001; Fig. 2). In contrast, the total time of immobility and the RMR were negatively correlated (Pearson's $r$=−0.428, $t_{298}$=−2.78, $P$<0.001; Fig. 3).

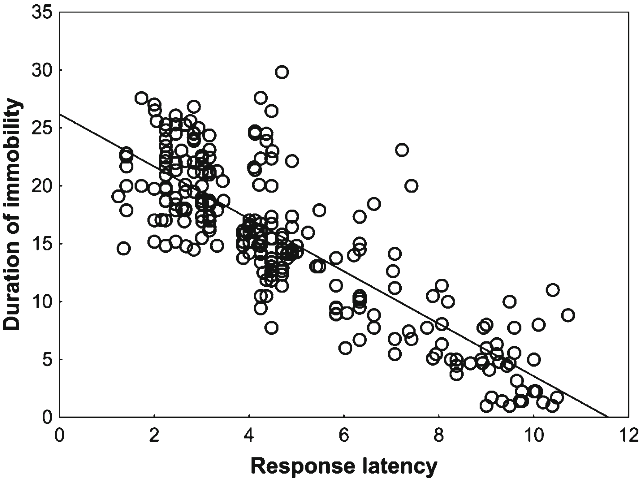

**Fig. 1** Negative correlation between the response latency to the mechanical stimulus and the duration of time spent motionless (Pearson's $r$=−0.83, $t_{298}$=−6.204, $P$<0.001) (all data were square root-transformed)

**Table 1** The effects of resting metabolic rate and sex on response latency and duration of immobility (GLM analysis) of mealworm beetles

| Source | *df* | Mean square | *F* | *P* |
|---|---|---|---|---|
| Response latency | | | | |
| Resting metabolic rate | 48,296 | 55,432.821 | 2.966 | 0.001 |
| Sex | 1,296 | 409.331 | 0.22 | 0.883 |
| Resting metabolic rate × sex | 32,296 | 4,648.392 | 0.241 | 0.999 |
| Total time spent immobile | | | | |
| Resting metabolic rate | 48,296 | 768,863.497 | 3.432 | 0.001 |
| Sex | 1,296 | 8,560.181 | 0.382 | 0.537 |
| Resting metabolic rate × sex | 32,296 | 13,097.395 | 0.585 | 0.963 |

### Predation experiment

On average, great tits preyed upon 7.63±0.77 beetles during each experimental trial, and only 71 out of 300 beetles survived. The number of female ($N$=40) and male survivors ($N$=31) appeared to be the same ($\chi^2$=1.181, *df*=1, $P$=0.28). Captured individuals had significantly higher RMR (74.42±42.03 VCO$_2$ μl h$^{-1}$, mean ± SD) than individuals that survived the predation trials (23.58±11.45 VCO$_2$ μl h$^{-1}$, mean ± SD) ($t$-test, $t$=22.32, $N_1$=229, $N_2$=71, $P$=0.01; Fig. 4). All of the survivors ($N$=71) became immobile once the predator was put in the arena, while most of the non-survivors (149 out of 229 individuals) remained active ($\chi^2$=89.1971, *df*=1, $P$=0.0001). The response latency to flicking of survivors (20.96±38.78 s, mean ± SD) was significantly shorter than the response latency of non-survivors (69.60±139.13, mean ± SD; $t$-test, $t$=−2.685, $N_1$=71, $N_2$=229, $P$=0.008). GLM analysis confirmed that higher RMR (Wald $\chi^2$=5.00, *df*=1, $P$=0.03) and longer response latency (Wald $\chi^2$=4.43, *df*=1, $P$=0.038) impaired the survival of mealworm beetles. The RMR by the response latency interaction was non-significant (Wald $\chi^2$=2.68, *df*=1, $P$=0. 092), showing that only beetles with greatest rates of the RMR and longer response latency to flicking were significantly more often attacked by predators. The total time spent motionless after flicking of survivors (277.48±163.90, mean ± SD) was significantly longer than that of non-survivors (186.04±174.15, mean ± SD; $t$-test, $t$=3.783, $N_1$=71, $N_2$=229, $P$=0.001).

## Discussion

The major novel finding of this study is that consistent individual differences in anti-predator behavior of male and female mealworm beetles were significantly correlated with their RMR and with survival. RMR was positively correlated with the latency of immobility response and was negatively correlated with the total duration of immobility, revealing a behavioral syndrome in the anti-predator behavior of *T. molitor*. These results suggest that individuals with higher levels of resting metabolic rate were bold, explaining their higher exposure to the risk of predation (Artacho and Nespolo 2009). This supports some recent findings showing that RMR may be positively related to mortality as evidenced in land snails, juvenile squirrels, and captive

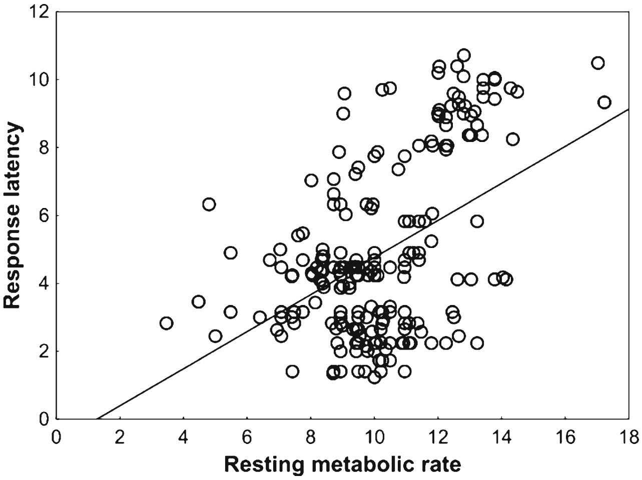

**Fig. 2** Positive correlation between resting metabolic rate and the response latency to predation risk (Pearson's $r$=0.489, $t_{298}$=4.517, $P$<0.001) (all data were square root-transformed)

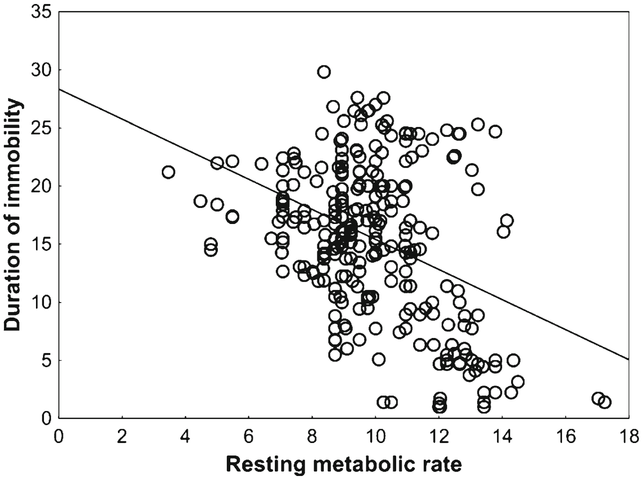

**Fig. 3** Negative correlation between resting metabolic rate and the total time spent immobile (Pearson's $r$=−0.428, $t_{298}$=−2.78, $P$<0.001) (all data were square root-transformed)

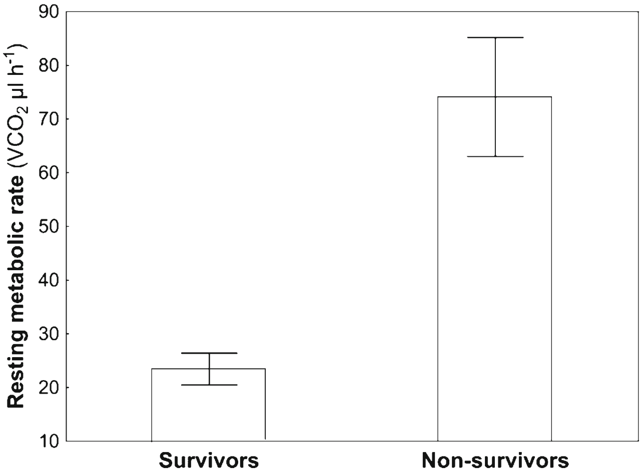

**Fig. 4** Resting metabolic rate of survivors and non-survivors. *Bars* show means ± SE

voles (Jackson et al. 2001; Alvarez and Nicieza 2005; Artacho and Nespolo 2009; Boratynski and Koteja 2009; Larivee et al. 2010; Smith and Blumstein 2010; Lantovį et al. 2011). We note that repeatabilities for our three main measures, while all statistically significant, ranged from 0.57 (RMR) to 0.85 (latency to become immobile). Although behavioral responses are typically thought to be more "plastic" than physiological reactions (West-Eberhard 2003), perhaps RMR is affected by some other important factors, which need to be studied in the future.

The results of this study support the hypothesis suggesting that consistent individual differences in energy metabolism might underlie consistent individual differences in behavior (Biro and Stamps 2008; Careau et al. 2008). Since energy is required to fuel all of the metabolic processes of the body, differences in energy metabolism may explain consistent individual differences in many behaviors, particularly those that are energetically costly (Schmidt-Nielsen 1991; Biro et al. 2010). Biro and Stamps (2008) suggested that consistent individual differences in resting metabolic rate might support consistent individual differences in growth and fecundity, in which case fast-growing and highly fecund individuals with higher resting metabolic rate should be more active, aggressive, and bold in contexts related to food acquisition (Burton et al. 2011).

It has been recently suggested that behavioral responses that require maximal aerobic output over brief periods of time, such as predator escape or activities related to mating, may be correlated with RMR (Sadowska et al. 2005; Wone et al. 2009). Some studies have revealed that in animals competing for food or feeding territories, individuals with higher RMR tend to be dominant (Metcalfe et al. 1995; Yamamoto et al. 1998). In contrast, in many laboratory settings, every individual has easy access to food ad libitum. In such cases, it is assumed that intake rate need not depend upon behavior, in which case one might not detect correlations between behavior and RMR or productivity. Indeed the ad libitum food accessibility in our laboratory setting might help explain the low (though significant) correlations between RMR and response latency (0.489) and between RMR and response duration (−0.428).

Empirical studies of the relationships between RMR and energy output across individuals, and the repeatability of such relationships, are rare. However, the first evidence has revealed positive correlations between metabolic rate and sustained energy output in different species (Chappell et al. 2004; Fu et al. 2005, 2008; Rezende et al. 2005, 2009; Vezina et al. 2006). Our results linked these relationships to fitness outcomes. Individuals with longer latency of immobility response, and with shorter total duration of time spent immobile, were consumed by great tits more often than less active individuals. We cannot tell exactly whether it was the long latency of anti-predator response or the short time spent motionless that increased the probability of being killed by the predator. However, it is clear that immediate digging in the layer of bran and staying immobile for several minutes was the most effective way to avoid predation by great tits. This unanswered question reflects a problem to be solved in the future. Since some beetles immediately stopped their activities under the risk of predation while others spent a few seconds to dig in the layer of bran, this may suggest different survival strategies of survivor beetles. We now need to determine whether anti-predator responses of the survivors represent different survival strategies and whether these strategies are related to metabolism.

High RMR has been shown to have fitness advantages in mating contexts. For example, locomotor activity is often energetically costly (Koteja 2000; Schmitz 2005; Yeates et al. 2007), and in the case of fighting (Kotiaho et al. 1998; Finerty et al. 2009) and courtship, aggressive defense of mates may also be energetically costly (Kotiaho et al. 1998). If increased rates of performance of these behaviors are advantageous, boldness may point to a positive link between reproductive success and RMR. It is generally known that males in most species achieve higher fitness by obtaining copulations with as many females as possible (Alcock 2001). In the *T. molitor* system, bold males may have more copulations than shy males because males should chase females to solicit copulations (Worden and Parker 2001). This could explain why bold males may have more chances to increase fitness prospects than their shy opponents (Godin and Dugatkin 1996; Smith and Blumstein 2008). Since a female *T. molitor* often mate repeatedly, and both precopulatory and postcopulatory behaviors are important components of sexual selection in this species (Worden and Parker 2001; Worden et al. 2005), it may mean that mate choice in *T. molitor* should be time- and energy-consuming also in female individuals. However, our results show a RMR-based trade-off between fitness benefits arising from high RMR and predation risk. It is important to note that artificial selection experiments have shown that there is heritable variation for length of death feigning in beetles, and when a predator is introduced, individuals selected for longer death feigning durations are at a selective advantage relative to those at shorter durations (Miyatake et al. 2004, 2009). A link between longer durations of death feigning and survival may provide some support for gene-based links between RMR and anti-predator behavior in *T. molitor*.

The results of this paper are consistent with a recently proposed hypothesis suggesting that personality traits may couple with life history traits and form integrative pace-of-life syndromes, where behavior and life history co-vary in a fast–slow lifestyle continuum (Réale et al. 2010). At the slow end of the lifestyle continuum, arising mainly from the general growth–mortality trade-off (Stamps 2007), individuals would have slow metabolism, low aggressiveness, and low boldness compared to individuals on the fast end of the continuum (Réale et al. 2010). In this scenario, the life history-driven consistency in animal behavior is ultimately caused by superior fitness of certain combinations of life history and behavior (Wolf et al. 2007; Dingemanse and Wolf 2010). For example, bold behavior should yield better fitness when combined with high metabolism and early rather than late maturation since higher mortality of bold individuals would make them unsuccessful in ever reaching the age required for late maturation. These predictions need to be tested in future studies since different combinations of life history and behavioral variables may yield equal expected lifetime fitness and thus explain the maintenance of different behavioral types in population (Biro et al. 2006; Dingemanse and Wolf 2010; Réale et al. 2010; Wolf and Weissing 2010).

**Acknowledgments** The study was supported by the Academy of Finland to M.J.R. and I.K., by the Estonian Ministry of Education and Science to R.M. (target-financing project number 0180004s09) and to M.M. and A.K. (target-financing project number SF0170057s09), by the Estonian Science Foundation Grant No. 7391 to M.M. and A.K., and by the European Social Fund within the project "Support for the implementation of doctoral studies at Daugavpils University" (agreement number 2009/0140/1DP/1.1.2.1.2./09/IPIA/VIAA/015) to I.K. and J.V. T.M.F. acknowledges the support of a Fulbright award during Spring 2012, which helped make his work on this manuscript possible.

## References

Alcock J (2001) Animal behavior: an evolutionary approach. Sinauer, Sunderland

Alvarez D, Nicieza AG (2005) Is metabolic rate a reliable predictor of growth and survival of brown trout (*Salmo trutta*) in the wild? Can J Fish Aquat Sci 62:643–649

Artacho P, Nespolo RF (2009) Natural selection reduces energy metabolism in the garden snail, *Helix aspersa* (*Cornu aspersum*). Evolution 63:1044–1050

Barnard C (2007) Ethical regulation and animal science: why animal behaviour is special. Anim Behav 74:5–13

Bell AM, Sih A (2007) Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol Lett 10:828–834

Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. Anim Behav 77:771–783

Bhattacharya AK, Ameel JJ, Waldbaue GP (1970) Method for sexing living pupal and adult yellow mealworms. Ann Entomol Soc Am 63:1783

Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history productivity? Trends Ecol Evol 23:361–368

Biro PA, Stamps JA (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends Ecol Evol 25:653–659

Biro PA, Abrahams MV, Post JR, Parkinson EA (2006) Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. J Anim Ecol 75:1165–1171

Biro PA, Beckmann C, Stamps JA (2010) Small within-day increases in temperature affects boldness and alters personality in coral reef fish. Proc R Soc B Biol Sci 277:71–77

Boratynski Z, Koteja P (2009) The association between body mass, metabolic rates and survival of bank voles. Funct Ecol 23:330–339

Burton T, Killen SS, Armstrong JD, Metcalfe NB (2011) What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proc R Soc B Biol Sci 278:3465–3473

Butler SJ, Whittingham MJ, Quinn JL, Cresswell W (2005) Quantifying the interaction between food density and habitat structure in determining patch selection. Anim Behav 69:337–343

Candolin U (1998) Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. Proc R Soc B Biol Sci 265:1171–1175

Careau V, Thomas D, Humphries MM, Réale D (2008) Energy metabolism and animal personality. Oikos 117:641–653

Castañeda LE, Figueroa CC, Bacigalupe LD, Nespolo RF (2010) Effects of wing polyphenism, aphid genotype and host plant chemistry on energy metabolism of the grain aphid, *Sitobion avenae*. J Insect Physiol 56:1920–1924

Chappell MA, Garland T, Rezende EL, Gomes FR (2004) Voluntary running in deer mice: speed, distance, energy costs and temperature effects. J Exp Biol 207:3839–3854

Cuthill IC (2007) Ethical regulation and animal science: why animal behaviour is not so special. Anim Behav 74:15–22

Daan S, Masman D, Strijkstra AM, Kenagy GJ (1990) Daily energy turnover during reproduction in birds and mammals: its relationships to basal metabolic rate. Acta XX Congr Int Ornithol IV:1976–1987

Dall SRX, Witter MS (1998) Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. Anim Behav 55:715–725

Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecol Lett 7:734–739

Daukste J, Kivleniece I, Krama T, Rantala MJ, Krams I (2012) Senescence in immune priming and attractiveness in a beetle. J Evol Biol 25:1298–1304

Dingemanse NJ, Réale D (2005) Natural selection and animal personality. Behaviour 142:1159–1184

Dingemanse NJ, Wolf M (2010) Recent models for adaptive personality differences: a review. Philos Trans R Soc B 365:3947–3958

Dohm MR (2002) Repeatability estimates do not always set an upper limit to heritability. Funct Ecol 16:273–280

Duncan FD (2003) The role of the subelytral cavity in respiration in a tenebrionid beetle, *Onymacris multistriata* (Tenebrionidae: Adesmiini). J Insect Physiol 49:339–346

Duncan FD, Byrne MJ (2005) The role of the mesothoracic spiracles in respiration in flighted and flightless dung beetles. J Exp Biol 208:907–914

Earle M, Lavigne DM (1990) Intraspecific variation in body size, metabolic rate, and reproduction of deer mice (*Peromyscus maniculatus*). Can J Zool 68:381–388

Fedigan LM (2010) Ethical issues faced by field primatologists: asking the relevant questions. Am J Primatol 72:754–771

Finerty SE, Wolt RC, Davis RW (2009) Summer activity pattern and field metabolic rate of adult male sea otters (*Enhydra lutris*) in a soft sediment habitat in Alaska. J Exp Mar Biol Ecol 377:36–42

Fu SJ, Xie XJ, Cao ZD (2005) Effect of fasting and repeat feeding on metabolic rate in southern catfish, *Silurus meridionalis* Chen. Mar Freshw Behav Physiol 38:191–198

Fu SJ, Cao ZD, Peng JL, Wang YX (2008) Is peak postprandial oxygen consumption positively related to growth rate and resting oxygen consumption in a sedentary catfish *Silurus meridionalis*? J Fish Biol 73:692–701

Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard—test of a model with foraging minnows. Ecology 68:1856–1862

Godin JGJ (1995) Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). Oecologia 103:224–229

Godin JGJ (1997) Evading predators. In: Godin JGJ (ed) Behavioural ecology of teleost fishes. Oxford University Press, New York, pp 191–236

Godin JGJ, Dugatkin LA (1996) Female mating preference for bold males in the guppy, *Poecilia reticulata*. Proc Natl Acad Sci USA 93:10262–10267

Gray EM, Bradley TJ (2006) Evidence from mosquitoes suggests that cyclic gas exchange and discontinuous gas exchange are two manifestations of a single respiratory pattern. J Exp Biol 209:1603–1611

Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. Neurosci Biobehav Rev 29:137–150

Gyuris E, Feró O, Tartally A, Barta Z (2011) Individual behaviour in firebugs (*Pyrrhocoris apterus*). Proc R Soc B Biol Sci 278:628–633

Hammond KA, Diamond J (1997) Maximal sustained energy budgets in humans and animals. Nature 386:457–462

Hammond KA, Wunder BA (1995) Effect of cold temperatures on the morphology of gastrointestinal tracts of two microtine rodents. J Mammal 76:232–239

Hammond KA, Lam M, Lloyd KCK, Diamond J (1996) Simultaneous manipulation of intestinal capacities and nutrient loads in mice. Am J Physiol Gastrointest Liver 271:G969–G979

Hayes JP, Garland T, Dohm MR (1992) Individual variation in metabolism and reproduction of *Mus*: are energetics and life history linked? Funct Ecol 6:5–14

Hedrick AV, Kortet R (2006) Hiding behaviour in two cricket populations that differ in predation pressure. Anim Behav 72:1111–1118

Hetz SK (1994) Untersuchung zu Atmung, Kreislauf und Säure-Basen-Regulation an Puppen der tropischen Schmetterlingsgattungen Ornithoptera, Troides and Attacus. Dissertation at Friedrich-Alexander-Universität, Erlangen-Nürnberg, p 216

Hollander FA, van Overveld T, Tokka I, Matthysen E (2008) Personality and nest defence in the great tit (*Parus major*). Ethology 114:405–412

Hõrak P, Lauri S, Ots I, Kollist H (2002) Repeatability of condition indices in captive greenfinches (*Carduelis chloris*). Can J Zool 80:636–643

Jackson DM, Trayhurn P, Speakman JR (2001) Associations between energetics and over-winter survival in the short-tailed field vole *Microtus agrestis*. J Anim Ecol 70:633–640

Jones KA, Godin J-GJ (2010) Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. Proc R Soc B Biol Sci 277:625–632

Karise R, Kuusik A, Mänd M, Metspalu L, Williams IH, Hiiesaar K, Luik A, Muljar R, Liiv K (2010) Gas exchange patterns of bumble bee foragers before and after exposing to lowered temperature. J Insect Physiol 56:529–535

Kivleniece I, Krams I, Daukste J, Krama T, Rantala MJ (2010) Sexual attractiveness of immune-challenged male mealworm beetles suggests terminal investment in reproduction. Anim Behav 80:1015–1021

Kortet R, Hedrick ANN (2007) A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. Biol J Linn Soc 91:475–482

Kortet R, Härkönen L, Hokkanen P, Härkönen S, Kaitala A, Kaunisto S, Laaksonen S, Kekäläinen J, Ylönen H (2010) Experiments on the ectoparasitic deer ked that often attacks humans; preferences for body parts, colour and temperature. Bull Entomol Res 100:279–285

Koteja P (2000) Energy assimilation, parental care and the evolution of endothermy. Proc R Soc B Biol Sci 267:479–484

Kotiaho JS, Alatalo RV, Mappes J, Nielsen MG, Parri S, Rivero A (1998) Energetic costs of size and sexual signalling in a wolf spider. Proc R Soc B Biol Sci 265:2203–2209

Krams I, Daukste J, Kivleniece I, Krama T, Rantala MJ (2013a) Previous encapsulation response enhances within individual protection against fungal parasite in the mealworm beetle *Tenebrio molitor*. Insect Science, doi:10.1111/j.1744-7917.2012.01574.x

Krams I, Daukste J, Kivleniece I, Kaasik A, Krama T, Freeberg TM, Rantala MJ (2013b) Trade-off between cellular immunity and life span in mealworm beetles *Tenebrio molitor*. Current Zoology 59 in press

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, New York

Lantovį P, Zub K, Koskela E, Sķchovį K, Borowski Z (2011) Is there a linkage between metabolism and personality in small mammals? The root vole (*Microtus oeconomus*) example. Physiol Behav 104:378–383

Larivee ML, Boutin S, Speakman JR, McAdam AG, Humphries MM (2010) Associations between over-winter survival and resting metabolic rate in juvenile North American red squirrels. Funct Ecol 24:597–607

Lessells CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. Auk 104:116–121

Lighton JRB (2008) Measuring metabolic rate: a manual for scientists. Oxford University Press, New York

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation—a review and prospectus. Can J Zool 68:619–640

Luttbeg B, Sih A (2010) Risk, resources and state-dependent adaptive behavioural syndromes. Philos Trans R Soc B 365:3977–3990

Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer, Sunderland

Macleod R, Gosler AG, Cresswell W (2005) Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. J Anim Ecol 74:956–964

Magnhagen C (1990) Reproduction under predation risk in the sand goby, *Pomatoschistus minutus*, and the black goby, *Gobius niger*, the effect of age and longevity. Behav Ecol Sociobiol 26:331–335

Mänd M, Kuusik A, Martin AJ, Williams IH, Luik A, Karise R, Metspalu L, Hiiesaar K (2005) Discontinuous gas exchange cycles and active ventilation in pupae of the bumblebee *Bombus terrestris*. Apidologie 36:561–570

Mänd M, Kuusik A, Martin AJ, Williams IH, Luik A, Karise R (2006) Regular periods of abdominal contractions recorded from larvae of the bumblebee, *Bombus terrestris* (Hymenoptera: Apidae). Eur J Entomol 103:319–322

McLean JA, Speakman JR (2000) Effects of body mass and reproduction on the basal metabolic rate of brown long-eared bats (*Plecotus auritus*). Physiol Biochem Zool 73:112–121

Metcalfe NB, Taylor AC, Thorpe JE (1995) Metabolic rate, social status and life-history strategies in Atlantic salmon. Anim Behav 49:431–436

Metspalu L, Kuusik A, Hiiesaar K, Tartes U (2002) Tonic immobility in adult Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) evoked by mechanical and optical stimuli. Eur J Entomol 99:215–219

Miyatake T, Katayama K, Takeda Y, Nakashima A, Sugita A, Mizumoto M (2004) Is death-feigning adaptive? Heritable variation in fitness difference of death-feigning behaviour. Proc R Soc B Biol Sci 271:2293–2296

Miyatake T, Nakayama S, Nishi Y, Nakajima S (2009) Tonically immobilized selfish prey can survive by sacrificing others. Proc R Soc B Biol Sci 276:2763–2767

Moret Y (2006) 'Trans-generational immune priming': specific enhancement of the antimicrobial immune response in the mealworm beetle, *Tenebrio molitor*. Proc R Soc B Biol Sci 273:1399–1405

Mueller P, Diamond J (2001) Metabolic rate and environmental productivity: well-provisioned animals evolved to run and idle fast. Proc Nat Acad Sci USA 98:12550–12554

Muljar R, Karise R, Viik E, Kuusik A, Williams I, Metspalu L, Hiiesaar K, Must A, Luik A, Mänd M (2012) Effects of Fastac 50 EC on bumble bee *Bombus terrestris* L. respiration: DGE disappearance does not lead to increasing water loss. J Insect Physiol 58:1469–1476

Nespolo RF, Franco M (2007) Whole-animal metabolic rate is a repeatable trait: a meta-analysis. J Exp Biol 210:2000–2005

Nespolo RF, Roff DA, Fairbairn DJ (2008) Energetic trade-off between maintenance costs and flight capacity in the sand cricket (*Gryllus firmus*). Funct Ecol 22:624–631

Niemelä PT, Vainikka A, Lahdenperä S, Kortet R (2012) Nymphal density, behavioural development, and life history in a field cricket. Behav Ecol Sociobiol 66:645–652

Niemelä PT, Vainikka A, Forsman JT, Loukola OJ, Kortet R (2013) How does variation in the environment and individual cognition explain the existence of consistent behavioural differences? Ecol Evol 3:457–464

Niewiarowski PH, Balk ML, Londraville RL (2000) Phenotypic effects of leptin in an ectotherm: a new tool to study the evolution of life histories and endothermy? J Exp Biol 203:295–300

Quinlan MC, Lighton JRB (1999) Respiratory physiology and water relations of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Physiol Entomol 24:293–302

Quinn JL, Cresswell W (2005) Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. Behaviour 142:1377–1402

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. Biol Rev 82:291–318

Réale D, Dingemanse NJ, Kazem AJN, Wright J (2010) Evolutionary and ecological approaches to the study of personality. Philos Trans R Soc B Biol Sci 365:3937–3946

Rezende EL, Chappell MA, Gomes FR, Malisch JL, Garland T (2005) Maximal metabolic rates during voluntary exercise, forced exercise, and cold exposure in house mice selectively bred for high wheel-running. J Exp Biol 208:2447–2458

Rezende EL, Gomes FR, Chappell MA, Garland T (2009) Running behavior and its energy cost in mice selectively bred for high voluntary locomotor activity. Physiol Biochem Zool 82:662–679

Ruxton GD, Sherratt TN, Speed MP (2004) Avoiding attack: the evolutionary ecology of crypsis, aposematism and mimicry. Oxford University Press, Oxford

Sadd B, Holman L, Armitage H, Lock F, Marland R, Siva-Jothy MT (2006) Modulation of sexual signalling by immune challenged male mealworm beetles (*Tenebrio molitor*, L.): evidence for terminal investment and dishonesty. J Evol Biol 19:321–325

Sadowska ET, Labocha MK, Baliga K, Stanisz A, Wroblewska AK, Jagusiak W, Koteja P (2005) Genetic correlations between basal and maximum metabolic rates in a wild rodent: consequences for evolution of endothermy. Evolution 59:672–681

Schmidt-Nielsen K (1991) Animal physiology. Cambridge University Press, Cambridge

Schmitz A (2005) Metabolic rates in harvestmen (Arachnida, Opiliones): the influence of running activity. Physiol Entomol 30:75–81

Sih A, Bell AM (2008) Insights for behavioral ecology from behavioral syndromes, chapter 5. In: Brockmann HJ, Roper TJ, Naguib M, Wynne-Edwards K, Barnard C, Mitani JC (eds) Advances in the study of behavior, vol 38. Academic, New York, pp 227–281

Smith BR, Blumstein DT (2008) Fitness consequences of personality: a meta-analysis. Behav Ecol 19:448–455

Smith BR, Blumstein DT (2010) Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). Behav Ecol 21:919–926

Speakman JR, Ergon T, Cavanagh R, Reid K, Scantlebury DM, Lambin X (2003) Resting and daily energy expenditures of free-living field voles are positively correlated but reflect extrinsic rather than intrinsic effects. Proc Natl Acad Sci 100:14057–14062

Speakman JR, Krol E, Johnson MS (2004) The functional significance of individual variation in basal metabolic rate. Physiol Biochem Zool 77:900–915

Stamps JA (2007) Growth-mortality tradeoffs and 'personality traits' in animals. Ecol Lett 10:355–363

Szafranska PA, Zub K, Konarzewski M (2007) Long-term repeatability of body mass and resting metabolic rate in free-living weasels, *Mustela nivalis*. Funct Ecol 21:731–737

Tartes U, Kuusik A, Vanatoa A (1999) Diversity in gas exchange and muscular activity patterns in insects studied by a respirometer-actograph. Physiol Entomol 24:150–157

Vainikka A, Seppala O, Loytynoja K, Rantala MJ (2006) Fitness consequences of female preference for male pheromones in *Tenebrio molitor*. Evol Ecol Res 8:943–957

Van Oers K, Drent PJ, de Goede P, van Noordwijk AJ (2004) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proc R Soc B Biol Sci 271:65–73

Vezina F, Speakman JR, Williams TD (2006) Individually variable energy management strategies in relation to energetic costs of egg production. Ecology 87:2447–2458

West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, New York

Wolf M, Weissing FJ (2010) An explanatory framework for adaptive personality differences. Philos Trans R Soc B Biol Sci 365:3959–3968

Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. Nature 447:581–584

Wone B, Sears MW, Labocha MK, Donovan ER, Hayes JP (2009) Genetic variances and covariances of aerobic metabolic rates in laboratory mice. Proc R Soc B Biol Sci 276:3695–3704

Worden BD, Parker PG (2001) Polyandry in grain beetles, *Tenebrio molitor*, leads to greater reproductive success: material or genetic benefits? Behav Ecol 12:761–767

Worden B, Skemp A, Papaj D (2005) Learning in two contexts: the effects of interference and body size in bumblebees. J Exp Biol 208:2045–2053

Yamamoto T, Ueda H, Higashi S (1998) Correlation among dominance status, metabolic rate and otolith size in masu salmon. J Fish Biol 52:281–290

Yeates LC, Williams TM, Fink TL (2007) Diving and foraging energetics of the smallest marine mammal, the sea otter (*Enhydra lutris*). J Exp Biol 210:1960–1970

Ylonen H (1994) Vole cycles and antipredatory behavior. Trends Ecol Evol 9:426–430

Zera AJ, Zhao ZW (2006) Intermediary metabolism and life-history trade-offs: differential metabolism of amino acids underlies the dispersal–reproduction trade-off in a wing-polymorphic cricket. Am Nat 167:889–900