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Sex differences in metabolic scaling exponents in American cockraoch, Periplaneta americana (L) (Blattodea: Blattidae)

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ABSTRACT

Background: Sexual differences in physiologies could results in significant variation in energy generation, allocation, and utilization among males and females organisms. Metabolic scaling exponents could as well be dimorphically varied in insects in which females are less active due to reproductive demands. This study investigated into the metabolic-mass scaling patterns of male and female American cockroach, *Periplaneta americana.*

Methods: Metabolic rate was measured indirectly by estimating the rate of oxygen consumption (VO_2) and carbon dioxide evolution (VCO_2) using manometric and titrimetric methods respectively. Least square regression was used to scale $Log_{10}VO_2$ with Log_{10}Mass and inferential statistics of analysis of variance, *t*-test, and coefficient of determinant (R^2) were used to test the goodness of regression slopes, compare slopes of regression lines, and test significance of the variance accounted for by each regression model, respectively, at $p < 0.05$.

Results: The results show that the metabolic rate was significantly correlated with body mass for males ($t_{24} = 67.8$), females ($t_{24} = 37.6$), and both sexes combined ($t_{49} = 22.4$). Each regression model was also significant; males ($F_{1, 48} = 69.7$), females ($F_{1, 48} = 261.4$), and both sexes combined ($F_{1, 98} = 88.9$). The slopes of males and females lines were significantly different ($t_{46} = 5.75$); however, the slopes of regression lines of both sexes combined was not significantly different from that of males ($t_{71} = 0.83$).

Conclusion: The results imply that there is a sexual difference in metabolic scaling exponents of cockroaches since their regression models cannot be represented by a single line due to differences in their intercept.

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1. Introduction

An organism metabolic rate is its fundamental biological attribute because it reflects a net difference between energy production and expenditure (Grodzicki and Walentnowicz, 2011). Metabolic rate reflects the cost of living under specific environmental conditions (Terblanche et al., 2005) and has been influenced by the environmental conditions under which organisms have evolved to thrive and reproduce (Piiroinen et al., 2010). In animals, metabolic rate can be determined either by measuring the rate of CO_2 production or the rate of O_2 consumption (Nespolo et al., 2003) and it scales allometrically according to

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the power function $R = aW^b$, where R is the metabolic rate, W the mass of the animal, b the mass exponent and a mass coefficient.

Scaling of organism metabolic rates with body mass has been a subject of interest in recent (Atanasov, 2010; Glazier, 2010; Piiroinen et al., 2010) and many have tried to explain the exponential value of the relationship. The exponent b being thought to be approximately 0.75 for the past century (Savage et al., 2004) has generated much debate about it universality (Enquist et al., 2007; Isaac and Carbone, 2010) or whether there is a taxon-specific variability (Clarke and Pörtner, 2010; White et al., 2009). However, there are ecological implications of variability in metabolic scaling among taxa (Glazier, 2005).

Recent findings show that no single scaling exponent is universal for all the animals (Atanasov, 2010; O' Connor et al., 2007). This is because many log–log metabolic scaling relationships are non-linear and cannot be represented by a single power function (Glazier, 2005). Variations in metabolic scaling have been associated with fitness in organisms (Ketola and Kotiaho, 2009) and viewed to be adaptive (Addo-Bediako et al., 2002; Davis et al., 2000). This, therefore, accounted for the substantial differences in intra and interspecific metabolic rates. Other reasons for variation in metabolic rate, especially in insects include mass (Gillooly et al., 2001), temperature (Terblanche and Chown, 2007), sex (Rogowitz and Chappell, 2000), age (Terblanche et al., 2004), season (McGaughran et al., 2009), activity (Gray and Bradley, 2003), altitude (Rourke, 2000), and climate (Nielsen et al., 1999). Despite such variation, the mean mass-specific metabolic rate is strikingly within a specific range across life's major domain as evidence of life's metabolic optimum (Makarieva et al. 2008).

Scaling of insects' metabolic rate is, therefore, subjected to the influence of many variables of which their levels of interactions define the power function b even within a population. It is sometime surprising that some of these factors such as sexual dimorphism are not much considered when making statement about intraspecific metabolic rate in insects (Atanasov, 2010; Nespolo et al., 2003) yet they could have profound influence on metabolic scaling variations among a population. This study therefore seeks to find the influence of sex on metabolic scaling in American cockroach, *Periplaneta americana*.

2. Materials and Methods

2.1. Study animal and rearing

Adult cockroaches *P. americana* (L) were collected from within a household in Ilorin (Longitudes 4° 30'and 4° 45' E and Latitudes 8° 25' and 8° 40' N) Kwara State, Nigeria. They were maintained in a paper carton of dimension (40 × 40 × 40 cm) in the Department of Zoology laboratory University of Ilorin, Ilorin at temperature (28°C ± 3°C) and Relative Humidity (75%–85%) on pulverized biscuit and water. Subcultures from individual ootheca were maintained to adult stage in a separate paper carton. Sexed reared adults of same age were retrieved from the culture for experimental purposes. In all cases, adult sexed roaches used for each experiment were from the same clutch (ootheca) and age. The roaches were isolated and starved for 12 hours (Blossman-Myer and Burggren, 2010; Piiroinen et al., 2010, Streicher et al., 2012), their masses were determined gravimetrically using Staton electronic balance (Model 36Bh; 600 ± 0.01 g) and subsequently subjected to respirometry assay.

2.2. Respiratory assay

Newly emerged adults (7 days old) of both sexes were used for the experiment. The oxygen consumption of each intact sexed resting cockroach was measured using a 75 ml Warburg manometric flask. The rate of oxygen consumption (VO_2) was monitored every 15 minutes over a period of 240 minutes using constant volume manometric technique using Brodie's fluid as the manometric fluid. The flask constant was calculated to be 6.81 and VO_2 was expressed as $\mu lO_2 mg^{-1} hours^{-1}$. The evolved CO_2 within the flask was trapped by 0.375M of potassium hydroxide located in a well within the respiratory chamber. The volume of CO_2 trapped (VO_2) by the Potassium Hydroxide was determined titrimetrically using a standard hydrochloric acid (Oriolowo and Ande, 2005) and expressed as $\mu lCO_2 mg^{-1} hours^{-1}$, while the respiratory quotient (RQ) was determined as a ratio of VCO_2 to VO_2.

2.3. Statistical analysis

An intraspecific mass scaling relationship between metabolic rate and body mass was calculated by a linear regression of metabolic rate ($Log_{10}VO_2$) on body mass ($Log_{10}W$) separately for male, female, and both sexes combined. The significance of each regression line was tested using F-test ($p < 0.05$), while the homogeneity of the regression lines was tested using t-test ($p < 0.05$). Moreover, the correlation coefficient of each regression line was tested using Pearson Moment Correlation Coefficient (r), while analysis of variance (ANOVA) was used to test the significance of oxygen consumption between male and female at ($p < 0.05$).

3. Results

The metabolic rate mass scaling equations obtained for males, females, and both sexes combined are given as follows:

$$VO_2 = 1.93W^{0.79} \quad (1)$$

$$VO_2 = 0.27W^{1.06} \quad (2)$$

$$VO_2 = 2.57W^{0.75} \quad (3)$$

where Equations (1–3) represent the scaling models for males, females, and male-female combined, respectively.

Metabolic rate was significantly correlated with body mass for males (t_{24} = 67.8, p < 0.05), females (t_{24} = 37.6, p < 0.05), and both sexes combined (t_{49} = 22.4, p < 0.05) (Table 1). Each regression line was significant ($F_{1, 48}$ = 69.7, $F_{1, 48}$ = 261.4, and $F_{1, 98}$ = 88.9; ANOVA; p < 0.05, respectively). The slopes of males and females regression lines were significantly different (t_{46} = 5.75, p < 0.05, homogeneity of slope models), slope of regression line of both sexes females were significantly (t_{71} = 4.78, p < 0.05 homogeneity of slope models); however, the slopes of regression line of both sexes was not significantly different from that of males (t_{71} = 0.83, p > 0.05, homogeneity of slope models). Therefore, males and females regression lines cannot be replace by a single line due to such significant difference in their slopes and intercepts.

The masses of males range between 605 and 1,653 mg, while that of females range between 910 and 1,853 mg and the mean mass of males and females are significantly different ($F_{1, 48}$ = 28.7, ANOVA, p < 0.05). Also, the mean respiratory rates (VO_2) of males and females were significantly different ($F_{1, 48}$ = 240.4, ANOVA, p < 0.05) (Table 2).

4. Discussion

The results of metabolic scaling exponents obtained from the two sexes of *P. americana* in this study show significantly different intraspecific gender variability. However, the exponents of 0.79 and 1.06, respectively, obtained for males and females, fall within the range of 0.79 and 1.29 reported for cockroaches (Chown et al., 2007). The differences obtained between the two sexes may probably be due to factors which act differentially among various life stages such as body mass and reproductive potential as reported in German cockroaches (Lee, 1994). The scaling exponents obtained in this study is consistent with 0.78 reported for metabolic scaling of eleven species of cockroaches (Coelho and Moore, 1989) as well as 0.83 reported by Chown et al. (2007), 0.83 for *Blaberus discoidalis* (Birchard and Arendse, 2001), while Gunn (1935) reported an exponent of 0.7–0.8 for *P. americana*, *Blatta orientalis*, and *Blatta germanica*. However, 0.53 and 0.49 reported for giant burrow cockroach (Xu et al., 2014) was much lower than those obtained in this study.

There was a significant difference in the metabolic rates of males and females cockroaches. Metabolic rate in male ranged between 0.44 and 0.54 $\mu lO_2 mg^{-1} hours^{-1}$ with an average of 0.49 $\mu lO_2 mg^{-1} hours^{-1}$ while in females it ranged between 0.40 and 0.44 $\mu lO_2 mg^{-1} hours^{-1}$ with an average of 0.42 $\mu lO_2 mg^{-1} hours^{-1}$. These values obtained were higher than 0.36 $\mu lO_2 mg^{-1} hours^{-1}$ and 0.31 $\mu lO_2 mg^{-1} hours^{-1}$ reported for *B. orientalis* and *P. americana* respectively (Gunn, 1935). However, they were lower when compared with 0.62 $\mu lO_2 mg^{-1} hours^{-1}$ reported for *B. germanica* (Hostetler et al., 1994). Differences between the values in this study and those reported earlier could be as a result

Table 1. Intraspecific mass scaling of metabolic rate (VO_2) and body mass (W) of cockroaches.

Sex	*b*	*a*	*r*	R^2	*n*	df	*p*
Males	0.79 ± 0.02**	1.93 ± 0.03	0.998	0.995**	25	1.24	0.05
Females	1.06 ± 0.01**	0.27 ± 0.02	0.992	0.984**	25	1.24	0.05
Both sexes	0.75 ± 0.03**	2.57 ± 0.05	0.955	0.913**	50	1.49	0.05

** Significant at p < 0.05.

Table 2. Mean metabolic rate of cockroaches.

Sex	VO_2 ($\mu lO_2 mg^{-1} hours^{-1}$)	Mass (mg)	RQ	*N*
Males	0.49 ± 0.02[a]	1,004.72 ± 226.16[a]	0.93	25
Females	0.42 ± 0.01[b]	1,368.64 ± 226.47[b]	0.98	25
Both sexes	0.45 ± 0.04[c]	1,186.68 ± 203.14[c]	0.96	50

Mean carrying different superscripts are significantly different (ANOVA, lLeast sSquare rRegression, p < 0.05).

of differences in temperature under which the experiments were carried out and the mean masses of cockroaches used. This study was conducted at a mean temperature of about 28°C while those reported earlier were conducted at about 25°C. Thus, as expected metabolic rate increases as temperature increases in ectotherms species like insects (Nespolo et al., 2003). Moreover, the average mass of cockroaches used in this study was 1,186.7 mg, whereas the average mass of cockroaches used by Hostetler et al. (1994) was 50 mg. This supports the fact that mass-specific metabolic rate increases with decrease body mass (Sears et al., 2012). Moreover, sexual differences exerted a significant influence on metabolic rate in *P. americana*.

Although RQ could only be used to predict the substrate being metabolizes (Withers, 1992). Generally, RQ values range from 1.0 for carbohydrate, 0.8 for protein, and 0.71 for lipid metabolism (Bartholomew, 1977). The RQ values of between 0.93 and 0.98 obtained from this study suggest that the carbohydrate served as the main metabolic substrate. This is actually the expected result because the cockroaches used for this study were fed only with biscuit and water.

5. Conclusion

In conclusion, there were differences between the metabolism of male and female cockroach, *P. americana.* The average oxygen consumption rate was higher in male than female and their metabolic scaling exponents differ markedly. Thus, sex difference plays a vital influence in the metabolic activities of this insect.

Conflict of interest

The authors declare no divergence of interest in this study.

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