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Are Pregnant Females of the German Cockroach Too Heavy to Run?

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How-Jing Lee (1994) Are pregnant females of the German cockroach too heavy to run? *Zoological Studies* **33**(3): 200-204. Pregnant females of the German cockroach, *Blattella germanica*, are highly inactive. Since pregnant female has to carry an ootheca which is > 30% of its body weight, the hypothesis that pregnant females are too heavy to run is proposed. If the energy costs were too high in pregnant females, it is possible that pregnant females were limited simply by high energy demand. To test this hypothesis, a reliable index of energy cost and oxygen consumption for pregnant females was used for comparison with non-pregnant females in either resting or running conditions. The oxygen consumption of pregnant females (14-day-old) was significantly less than that of newly emerged females. The same age virgin females with an extra weight did not significantly increase oxygen consumption when compared to virgin females without an extra weight. No positive correlation was found between a heavy load on females and oxygen consumption. 14-day-old females could sustain heavy loads without raising their oxygen consumption. From these results, it is concluded pregnant females are not bound by the heavy load of the ootheca to become inactive, and the hypothesis is falsified.

Key words: *Blattella germanica*, Oxygen consumption.

Females of the German cockroach, *Blattella germanica*, produce and carry oothecae to protect eggs from dehydration and enemies (Schal et al. 1984). Pregnant females (carrying oothecae) significantly reduce their daily locomotion and food consumption (Lee and Wu 1994). These phenomena have been interpreted as the results of low nutrient demand of resting ovaries (Roth and Stay 1959, Cochran 1983). Since the ootheca requires a great deal of energy to make and it weighs about 30% of the fresh body weight (Mullins and Cochran 1986), it is possible that the heavy weight of ootheca forced the pregnant females to decrease locomotion in order to prevent exhaustion.

The purpose of this study is to investigate the possibility that pregnant females are forced to reduce locomotion in order to sustain the heavy energetic load of carrying ootheca. Since locomotion requires aerobic metabolism of energy source, the oxygen consumption appears to be a reliable index of energy cost. By comparing pregnant females' energy costs with non-pregnant females', whether or not the heavy load of the ootheca is a limiting factor of locomotion can be demonstrated. In this study, oxygen consumption by pregnant and non-pregnant females either resting or running was measured and compared to answer the question "Are pregnant females of the German cockroach too heavy to run?".

MATERIALS AND METHODS

The German cockroaches, *Blattella germanica* were collected from households in Taipei, Taiwan and reared in the laboratory for several generations. Cockroaches were kept in 4 L transparent plastic jars with screen lids. Dog food and water were provided ad libitum. Several pieces of Styrofoam were added to provide shelter for the cockroaches. Late-instar nymphs were removed and reared en masse in transparent plastic cups (9.5 dia. × 5.5 cm). Upon reaching adulthood, cockroaches were separated daily by sex and kept under the same conditions. The culture was reared at 28°C, 16L:8D conditions.

Cockroach oxygen consumption was measured with an open flow respirometer which consisted of a flow control (Ametex, R-2), oxygen sensor (Ametex, N-37), and an oxygen analyzer (Ametex, S-3A/II). At a flow rate of 75 ml/min, the air leaving the test chamber passed through a filter containing Drierite to absorb water vapor, then it passed into the oxygen sensor for oxygen concentration measurement. Control air flow with no cockroach in the test chamber passed through the same experiment setup. Oxygen consumption was calculated as follows:

$$VO_2 \text{ (ml/hr/g)} = \text{Flow rate (ml/min)} \times 60 \text{ (min/hr)} \times (O_{2(\text{test-empty})}\%/100)/\text{Body mass (g)}$$

A respirometer and a thermal couple interfaced with a personal computer were used to register the continuous oxygen consumption (10 samplings per second) and temperature (room temperature) changes. Since the quantity of gas held by a given volume varies as a function of temperature, pressure and water vapor content, oxygen consumption was standardized using STPD (Standard Temperature Pressure Dry). To transform a volume into STPD condition, the following formula was used:

$$V_2(\text{STPD}) = P_1/P_2 \times T_2/T_1 \times V_1$$

where $V_1 = VO_2$ uncorrected, P_1 = barometric pressure (torr), T_1 = experimental temperature°C + 273.15°K, T_2 = 273.15°K, P_2 = 760 torr, no water vapor.

Newly emerged adult females were weighed individually and placed in a test chamber (50 ml) to measure the oxygen consumption while at rest. The same individual was also placed on a various-speed treadmill to force running (average speed 6.3 m/min). Air passing through the treadmill test chamber was monitored for oxygen consumption. When females reached 6-day-old, one group of females were allowed to mate with sexually mature males, while the other group was kept virgin. Oxygen consumption during resting and running of pregnant females (5 days after ootheca extrusion) were measured . An extra weight (paraffin-filled ootheca = 34 mg) was glued onto the pronotum of virgin females (5 days after 1st non-viable ootheca dropped). The oxygen consumption of the virgin females with and without the extra weight were also measured during resting and running.

RESULTS

The effects of age on the oxygen consumption are illustrated in Fig. 1. Newly emerged females have a significantly high energy demand during rest (2.23 ± 0.37 O_2 ml/h/g) ($p < 0.0001$, ANOVA) but not while running (2.94 ± 0.86 O_2 ml/h/g) ($p > 0.143$, ANOVA) conditions. When females reached the sexual receptive stage (6-day-old), the energy demand (1.69 ± 0.44 O_2 ml/h/g during rest, 2.58 ± 0.94 O_2 ml/h/g while running) dropped significantly. Moreover, females had low energy demands (1.80 ± 0.35 O_2 ml/h/g during rest, 2.38 ± 0.92 O_2 ml/h/g while running) during pregnancy (14-day-old). Running required a significant increase in oxygen consumption regardless of the female's age, when compared with the energy demands during rest ($p < 0.001$, 0.0001, or 0.01 for 0-, 6-, or 14-day-old females, respectively, Student *t*-test). The oxygen consumption while running was 1.3, 1.5, or 1.3 times higher than it during rest for 0-, 6-, or 14-day-old females, respectively.

The effect of carrying an ootheca or extra weight on the oxygen consumption of 14-day old females is shown in Fig. 2. Regardless of mating status, 14-day old females can carry a heavy load. Oxygen consumption while at rest was similar among mated females with an ootheca (1.90 ± 0.35 O_2 ml/h/g), non-mated with an extra weight (1.80 ± 0.35 O_2 ml/h/g), and non-mated without an extra

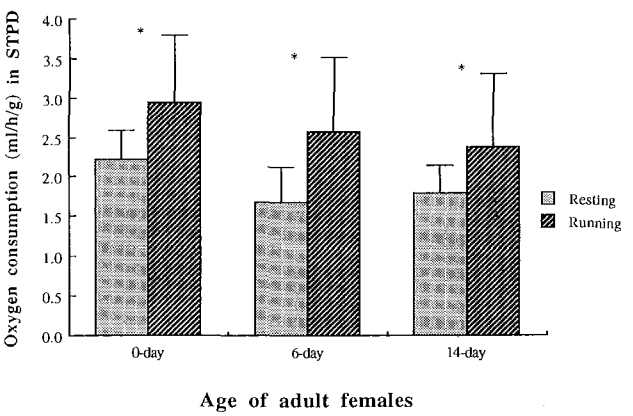

Fig. 1. The effects of age on oxygen consumption of the German cockroach, *Blattella germanica*, while either resting or running. Each vertical bar represents one set of standard error (n = 21 for each age group). "*" on the histogram indicates a significant difference between resting and running at p = 0.001, 0.0001, or 0.01 for 0-, 6-, or 14-day-old females, respectively (Student *t*-test). While resting only 0-day-old females have a significantly higher oxygen consumption than either 6- or 14-day-old females ($p < 0.0001$, Least Significant Difference test). However, there is no significant difference of oxygen consumption among females while running ($p > 0.143$, ANOVA).

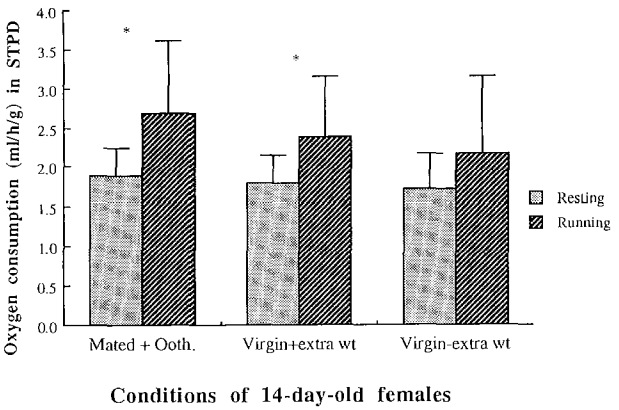

Fig. 2. Oxygen consumption changes in the 14-day-old female German cockroach, *Blattella germanica*, with different mating status or carrying load. Each vertical bar represents one set of standard error (n = 10 for each condition). "*" on the histogram indicates a significant difference between resting and running at p = 0.01, 0.02, or 0.17 for Mated with Ooth., Virgin with extra wt, or Virgin without extra wt females, respectively (Student t-test). There is no significant difference in oxygen consumption among 3 conditioned females while either resting or running at $p > 0.01$ (ANOVA).

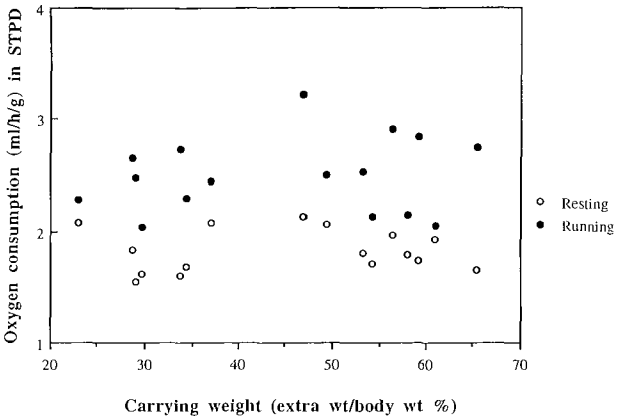

Fig. 3. Relationship between oxygen consumption and carrying load of 14-day-old females of the German cockroach, *Blattella germanica* (n = 18). There is no positive correlationship ($p > 0.01$, Linear Regression Analysis) between carrying extra weight and oxygen consumption for the females.

weight (1.72 ± 0.44 O_2 ml/h/g). Although all three-conditioned females increased their oxygen consumption while running, virgin females without an extra weight did not have a significant increase in oxygen consumption ($p > 0.17$, Student t-test) when they were moved from resting to running (2.17 ± 0.98 O_2 ml/h/g). Still, all the females in all 3 conditions exhibited the same energy demand requirement while running, and the oxygen consumption increase from resting to running were also the same ($p > 0.01$, ANOVA). Therefore, the results did not show convincingly that females carrying an ootheca or an extra weight demanded a significant increase in oxygen consumption (Fig. 2).

The weight which a female carries affects its oxygen consumption at rest or while running (Fig. 3). There is no positive correlation ($p > 0.01$, Linear Regression Analysis) between the percentage of the extra weight against fresh body weight and oxygen consumption. The results show that females carrying an extra weight up to 65% of their body weight did not significantly affect their oxygen consumption, although oxygen consumption did increase when females were moved from resting to running ($p < 0.0001$, Student t-test). It appears that 14-day old females can sustain a lot of extra weight without significantly increasing oxygen consumption.

DISCUSSION

Cockroaches are highly specialized for terrestrial locomotion (Herreid et al. 1981a), and some, such as in the case of the German cockroach, have lost their ability to fly altogether. Since the German cockroach showed a cyclic pattern of reproduction (Lee and Wu 1994), its locomotive activity coincided with its reproductive cycle. Female adults became highly active when they were sexually receptive (5-8 days old). Although the body mass of sexually receptive females is significantly larger than newly emerged females (Wu 1992), there is no significant difference in oxygen consumption during running (Fig. 1). However, sexually receptive females required less energy during rest when compared with newly emerged females. These findings may be contributed to the age related metabolic rate differences or simply the mass difference that small animals (newly emerged females) use more metabolic energy per unit mass than large animals (6-day-old females) to run on a level surface (Full and Tullis 1990).

Once a female went into pregnancy, its locomotive activity became minimum (Lee and Wu 1994). Although pregnant females carry the heavy load of an ootheca (at least 30% of its body weight), its oxygen consumption while running did not reflect a proportional energy requirement increase for carrying the extra weight (Fig. 1). A pregnant female spent significantly less energy in locomotion when compared to a newly emerged female whose body weight is much smaller. This finding

may contradict the hypothesis that pregnant females are too heavy to run. Other factors, such as predator avoidance and dehydration prevention (Schal et al. 1984) may be the more important limiting factors that force pregnant females to shelter until its eggs have hatched from its ootheca.

Pregnant females can undergo a period of starvation without affecting its own and offspring's survival when only water is provided (Durbin and Cochran 1985, Wu 1992). A starvation period can cause a depression of energy metabolism (Slansky and Scriber 1985) evidenced by reduced oxygen consumption (May 1989). Low oxygen consumption in pregnant females may be contributed to starvation or non-feeding periods. This phenomenon may indicate a physiological mechanism which prevents pregnant females from active locomotion; the heavy load of an ootheca is not the limiting factor to keep pregnant female dormant.

When females were 14 days old, regardless of their mating status or burden, they showed similar energy requirements for either rest or running (Fig. 2). Fourteen day old virgin females did not show active metabolism since their ovarian development was still at rest (Wu 1992); therefore, at this age, mated and virgin females had basically similar metabolic rates. From the small oxygen consumption increase from resting to running, it is clear that the German cockroach is quite energy efficient while running compared to other cockroaches (Herreid et al. 1981b, Herreid and Full 1984). This finding may partially explain its agile response to environmental stimuli (personal observation).

Yox et al. (1982) found that passive resting tension in the leg muscles of arthropods maintains limb position. This passive tension in the limb of quiescent cockroaches could provide an energetically inexpensive mechanism for maintaining posture, regardless of the resting angle. Full and Tullis (1990) also found that the use of skeletal structures to maintain position would require no additional muscle force production, making any added gravitational effects energetically insignificant. These findings may partially explain why the oxygen consumption of females carrying extra weight did not show a positive correlation with increasing extra weight (Fig. 3). Although oxygen consumption did increase while running, no positive correlationship with increasing extra weight was found. This phenomenon may also contribute to the skeletal structures of the cockroach which can carry itself easily without raising its energy requirement.

It was obvious that pregnant females did not increase their energy consumption along with her body weight. The results indicated that pregnant females were energy efficient without energy deficiency problem while running (Figs. 1-3). Based on the oxygen consumption data presented in this study, it is reasonable to conclude that heavy load of an ootheca is not a key factor that limits pregnant female's locomotive activity.

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懷孕的德國蜚蠊是否太重而跑不動？

李 後 晶[1]

懷孕的德國蜚蠊活動量很低。因爲懷孕的雌蟲須要背負相當本身體重百分之三十以上的卵鞘，所以有一假說的提出：懷孕的德國蜚蠊身體太重而跑不動。本研究由雌蟲在休息或奔跑時氧氣消耗量來測試這個假說。懷孕雌蟲（14日齡）的氧氣消耗量比剛羽化雌蟲顯著地少，當將重量加在同日齡之處女雌蟲，並不會增加其氧氣消耗量。因爲增加重量與氧氣消耗量的改變並不呈正相關，14日齡雌蟲可以背負重擔而不增加其氧氣消耗量。從這些結果得知，懷孕雌蟲並不受背負卵鞘重量之影響而變得不活躍，所以否証了這個假說。

關鍵詞：德國蜚蠊，氧氣消耗量。

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