Metabolism and allometric scaling of the infraorder Acrididea, including four grasshopper species of the Australian Wet Tropics (suborder Caelifera)

Zoe Hills[1]

Abstract

The routine metabolic rate of four grasshopper species of the suborder Caelifera, *Valanga irregularis*, *Austacris guttulosa*, *Oxya japonica* (Family Acrididae) and *Atractomorpha similis* (Pyrgomorphidae), collected from around the Daintree Rainforest Observatory, Australia, was measured. This data was supplemented with data from other species in the literature to investigate the relationship between mass and metabolic rate in the Acrididae family, and how closely it followed Kleiber's law. The difference in metabolic efficiency (metabolic rate/mass) between *V. irregularis* and *A. guttulosa* was also investigated. *Austacris guttulosa* is a pest species, and information about its metabolism may contribute to the development of control programs. Metabolic rate and mass had a power relationship of 0.97, higher than the 0.75 predicted by Kleiber's law. There was no significant difference in the metabolic efficiency of *A. guttulosa* and *V. irregularis*.

Key Words: allometry, grasshopper, locust, Acrididea

Introduction

Metabolic rate is an important characteristic of an organism and varies both between and within species. One of the causes of this variation is the mass of the organism. The effect of mass on metabolism is often expressed by the allometric equation $Y = aM^b$, where Y stands for the metabolic rate, a is a scaling constant, M is the mass, and b is the power that controls the relationship (Niklas and Kutschera 2015). Metabolic rate does not scale one to one with mass. Early on in the study of how mass relates to biological characteristics (allometry), the power term was estimated to be 2/3, similar to the relationship between surface area and volume (Sousa *et al.* 2008). However, Kleiber found that in many cases the relationship is closer to ¾, which became known as Kleiber's law (Niklas and Kutschera 2015). Kleiber's law is generally found to be true when comparing organisms with very different masses but tends not to hold as strongly between species of similar mass or that are closely related (Chown *et al.* 2007).

The metabolic rate of abundant species, including grasshoppers, can have a large effect on the ecosystem as a whole. Grasshoppers have a major impact on ecosystems, as they

---

[1] Corresponding author: u5791138@anu.edu.au, Research School of Biology, ANU, Canberra, ACT, Australia

are often one of the most abundant herbivores. Grasshoppers consume large amounts of plant biomass, and have been shown to eat different plants depending on what environmental stresses they are under (Hawlena and Schmitz 2010). Grasshopper faeces are a major food source for detritivores, and their specific diet affects the nutrient cycling within the system (Hawlena and Schmitz 2010). Some grasshopper species are well studied and often used as laboratory models; for example, *Schistocerca americana* (Greenlee and Harrison 2004; Groenewald *et al.* 2014).

Four of the species in this study, *Valanga irregularis, Austacris guttulosa, Oxya japonica* and *Atractomorpha similis*, are found in the Australian Wet Tropics. *Valanga irregularis* is the largest grasshopper in Australia and is solitary (Milner *et al.* 1996). *Austacris guttulosa*, commonly known as the spur throated locust, is a large, swarming species that can jump and fly relatively long distances (Milner *et al.* 1996). While it is not as damaging as some other locust species, it is a pest species that can damage grain crops (Murray *et al.* 2013). *Oxya japonica* primarily eats grasses, and is also potentially a pest species, often damaging rice crops (Trisnawati *et al.* 2015). *Atractomorpha similis* is found in temperate to tropical areas of Australia, and prefers damp conditions (John and King 1983). Knowledge of the metabolic rate of both pest and non-pest species, and what factors affect their metabolism, may be important for developing pest control programs, as well as providing a greater understanding of ecosystems generally.

The aim of this study was to investigate the relationship between mass and metabolic rate within the Acrididea infraorder, which includes grasshoppers of the Australian Wet Tropics. This investigation draws on data from multiple sources, including original research on the less studied species from the Australian Wet Tropics. This study also investigated the difference in metabolic efficiency between *V irregularis* and *Austacris guttulosa*. Across species, it was predicted that Kleiber's law would be followed, and metabolic efficiency would be related to a power of ¾. It was also hypothesised that *A. guttulosa* would have a different metabolic rate to *V. irregularis*.

Methods

Grasshoppers were collected from long grass in and around the Daintree Rainforest Observatory (Cape Tribulation, Queensland, Australia), using nets. These grasshoppers were transferred into labelled specimen jars. Multiple species were collected; however, there was a focus on collecting specimens of *A. guttulosa* and *V. irregularis*. Species were identified using the Observatory's insect collection. Grasshoppers were sexed by examining the end of their abdomen; females would have either an ovipositor or a non-pointed end on their abdomen.

The specimens were then weighed, and their mass recorded. Their length and width at the widest and narrowest points were measured with Vernier calipers. The widths were then averaged, and the volume of the grasshoppers estimated by $\pi r^2 h$, where r was half the average width, and h was the length of the grasshoppers. This method has potential advantages over estimating volume by assuming 1 g of body mass is equivalent to 1 mL of volume because it makes no assumptions about density. However, where length and width could not be measured, the assumption of 1 g of body mass approximating 1 mL of volume was used.

A FireSting Oxygen Logger was used to measure oxygen consumption. Specimens were placed into the tubes of the logger. The grasshoppers were not fasted prior to measurement. Temperature varied between 23.7°C and 27.2°C. The tubes were kept open for approximately 5 minutes to allow for the oxygen concentrations to equalise and for the grasshoppers to become less active. After 5 minutes, the tubes were closed at the same time, and the oxygen concentration logged for 15 minutes. Measurements were taken every 15 seconds for the first minute, then once every 3 minutes afterwards. The volume of the FireSting Oxygen Logger tubes was measured by filling them with water, and transferring the water into a measuring cylinder. The oxygen logger had a volume of 220,000 mm^3, and was made of glass.

The oxygen consumption was calculated by taking the air volume (the volume of the jar minus the volume of the insect) and multiplying it by the percentage of oxygen consumed, then divided by 100. This gave the oxygen consumed in cubic millimetres. Metabolic rate was calculated by taking the cubic millimetres of oxygen consumed and dividing it by the 15-minute run time to give cubic millimetres of oxygen consumed per minute.

Data from other papers was used for comparison, with preference for metabolisms of adult specimens measured at approximately 25°C . Data on adult *Schistocerca americana* specimens from Greenlee and Harrison (2004) were included, and the reported values in micromoles of CO_2 produced were converted into cubic millimetres of O_2 consumed by assuming first that CO_2 production = O_2 consumption, and second that measurements were made at approximately standard temperature and pressure for ease of converting moles to volume. Data from Fielding and DeFoliart (2008) were converted from J/hr to mL O_2/hr by dividing it by 20.1, as this is the inverse of the procedure Fielding and DeFoliart used to convert directly measured mL O_2 consumed/hr to J/hr. This mL/hr was then converted to mm^3/min by multipling by 1,000 and then dividing by 60.

Species in this study with greater than 4 samples had their mass and metabolic rate averaged, and plotted on a log-log plot. Data from Greenlee and Harrison (2004) and Fielding and DeFoliart (2008) were also plotted on this log-log plot. A linear regression was performed on this plot to find the scaling component, which is the gradient of the log-log plot. The gradient of the linear regression is the same as the exponent of the relationship between mass and metabolism.

A two-tailed Student's t test assuming unequal variance was performed to compare the metabolic efficiency (metabolic rate/mass) of *Austacris guttulosa* and *Valanga irregularis*. These two species were compared because they were similar in size and a relatively high number of individuals were collected from the field. However, despite their similar size and habitat, *A. guttulosa* is an agricultural pest, sometimes forming large plagues, while *V. irregularis* is a solitary, non-pest species (Milner *et al.* 1996). The purpose of the comparison was to determine whether the different behaviours of the species were reflected in their metabolic rates. Metabolic efficiency was compared to control for the direct effect of mass on metabolism (i.e. the fact that larger individuals would have a higher metabolism than smaller individuals). While *V. irregularis* and *A. guttulosa* individuals were similar in size, they were not identical, so mass had to be controlled for. A *t*-test assuming unequal variance was chosen, as an *F* test showed the variance was unequal between *A. guttulosa* and *V. irregularis*.

Results

Table 1: A summary of samples

Species	Number sampled	Source/citation
Atractamorpha similis	3	Daintree Rainforest Observatory (Cape Tribulation, Queensland, Australia)
Austracris guttulosa	18	Daintree Rainforest Observatory (Cape Tribulation, Queensland, Australia)
Oxya japonica	5	Daintree Rainforest Observatory (Cape Tribulation, Queensland, Australia)
Valanga irregularis	7	Daintree Rainforest Observatory (Cape Tribulation, Queensland, Australia)
Schistocerca americana	16	Lab reared from eggs at Arizona State University (Greenlee and Harrison 2004)
Chorthippus dubius	Unknown	Fielding and DeFoliart (2008)
Bootettix punctatus	Unknown	Fielding and DeFoliart (2008)
Melanoplus sanguinipes	25	Raised indoors from descendents of specimens collected near Delta Junction, Alaska, United States of America (Fielding and DeFoliart 2008)
Melanoplus complanipes	Unknown	Fielding and DeFoliart (2008)
Melanoplus bivittatus	Unknown	Fielding and DeFoliart (2008)
Trimertropis saxatalis	Unknown	Fielding and DeFoliart (2008)
Trimertropis sufusa	Unknown	Fielding and DeFoliart (2008)
Trimertropis pallidipennis	Unknown	Fielding and DeFoliart (2008)
Arphia psuedonietana	Unknown	Fielding and DeFoliart (2008)
Arphia conspersa	Unknown	Fielding and DeFoliart (2008)
Xanthippus corallipes	Unknown	Fielding and DeFoliart (2008)
Encoptolophus sordidus	Unknown	Fielding and DeFoliart (2008)
Schistocerca gregaria	Unknown	Fielding and DeFoliart (2008)

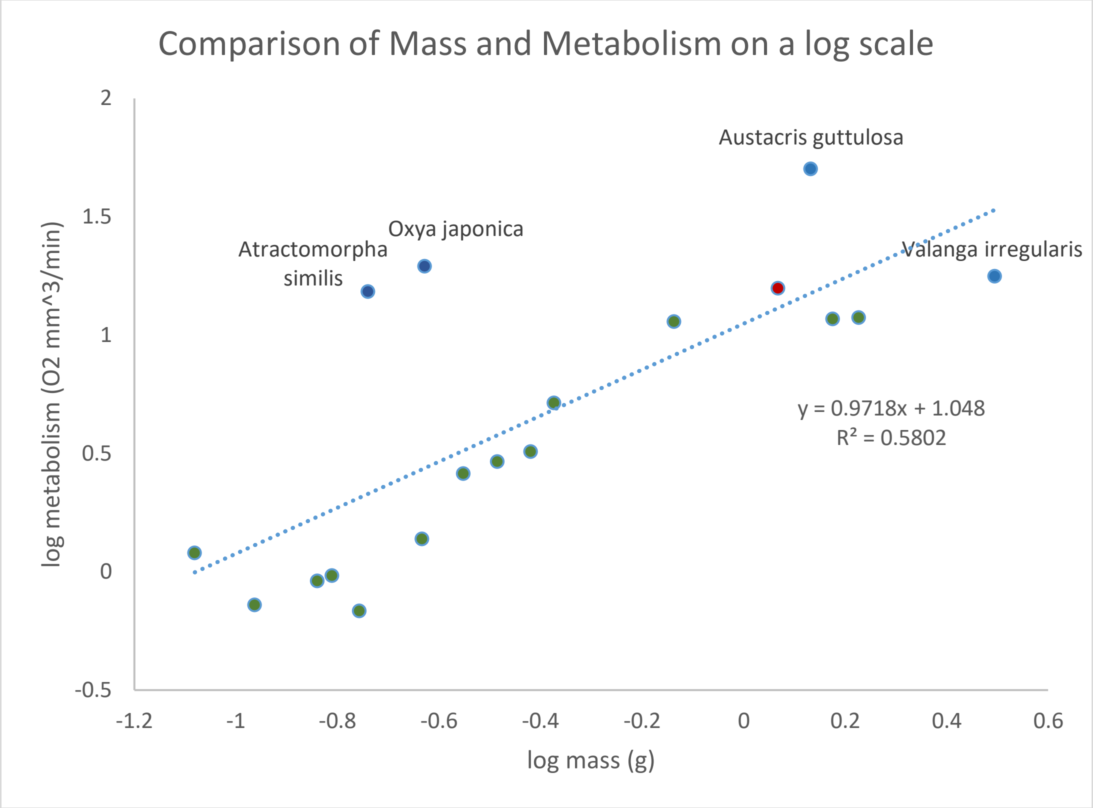

Figure 1: A linear regression of the log metabolism and mass of various Acrididae species. The four labelled blue points are the species measured in this study. The red point is data for *Schistocerca americana* from Greenlee and Harrison (2004). The green points are data collected by Fielding and DeFoliart (2008).

The gradient term of the linear regression of the log-log plot of metabolic rate vs mass was 0.9718. This means the scaling term of metabolic rate compared to mass is $Y=aM^{0.9718}$ in the case of the species studied. The R^2 of the linear regression was 0.5802.

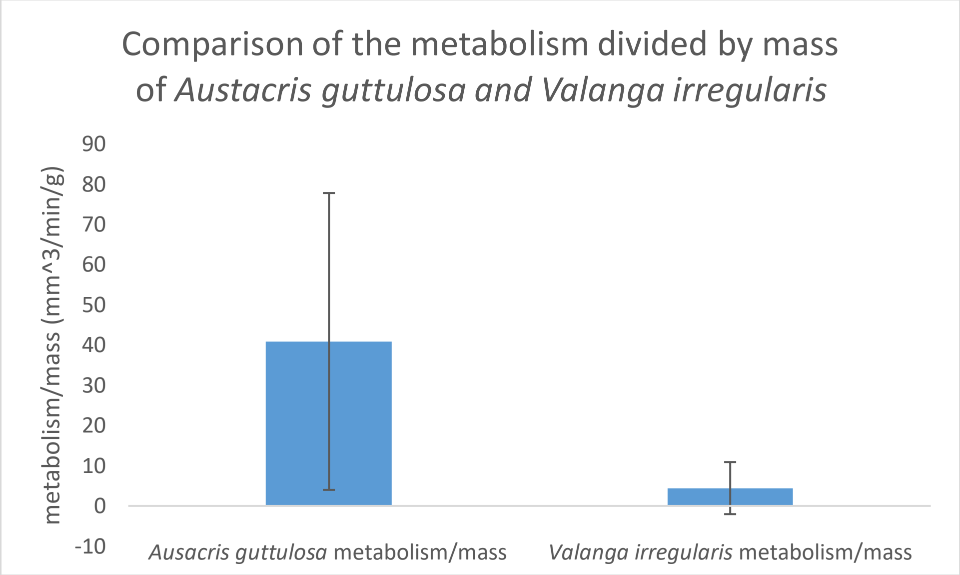

Figure 2: A comparison of metabolic rate/mass between *Valanga irregularis* and *Austacris guttulosa*. Error bars are for standard error.

The *p*-value of the *t*-test comparing the metabolic efficiency of *A. guttulosa* and *V. irregularis* was 0.36, which was higher than 0.05, therefore the result was not significant. While the average metabolism/mass of *A. guttulosa* was higher (40.89 mm^3/min/g) than

V. irregularis (4.44 mm^3/min/g), the variance within *A. guttulosa* was high (36.90; Figure 2).

Discussion

A power relationship of 0.97 between mass and metabolic rate was found. This is higher than the 0.75 predicted by Kleiber's law. However, the 0.75 power relationship found by Kleiber generally applies to unrelated species with very different masses, and often does not apply among species of similar size, or those that are related to each other (Chown *et al.* 2007). The species investigated in this study belong to the Acrididea infraorder, and only varied in mass between 0.11 and 5.61 g. In studies looking at insects as a whole, a power relationship of 0.82 was determined, and values between 0.67 and 1.0 were found intraspecifically (Chown *et al.* 2007). While this study was interspecific, given the relatively close relationship between many of the species it is plausible that the value of the mass–metabolism power relationship is further from the 0.75 predicted by Kleiber's law.

An R^2 value of 0.58 is not particularly high, but in the context of this study is fairly reasonable. Over 50 per cent of the variation in metabolism is correlated with mass. Considering the many potential causes of variation in metabolism, having over 50 per cent of the variation correlated with one variable is notable. Three of the four species measured in this study, *A. guttulosa, O. japonica* and *A. similis*, had metabolic rates that lay substantially above the regression line (Figure 1). This could be due to species from the Australian Wet Tropics having a higher metabolism compared to other Acrididea species of similar mass. Alternatively, it could be caused by the fact that while in other studies the specimens were fasted before metabolism was measured, in this study, due to time constraints, they were not.

We found no significant difference in metabolic efficiency between *A. guttulosa* and *V. irregularis* due to the high variance of *A. guttulosa*. The cause of this high variance is not known. There was no significant difference in the metabolic efficiency between male and female *A. guttulosa* individuals, so sex differences or the difference between gravid and non-gravid individuals were unlikely to be the cause of the variance. There could be some other causal factor, such as specimens having last eaten at different times or some environmental factor. Or, *A. guttulosa* metabolism may just be somewhat variable due to some other currently unknown biological factor.

This study is important due to the ecological importance of grasshoppers. They are some of the most abundant herbivores in many ecosystems. Their metabolism, and thus the amount of food they consume, has large ecosystem effects, which are only amplified by their abundance. Additionally, *Austacris guttulosa* and *Oxya japonica* are pest species (Murray *et al.* 2013, Trisnawati *et al.* 2015). Knowledge of their metabolic rates, especially compared to other grasshopper species, may be useful in developing control measures.

There have been previous individual and comparative studies of *Austacris guttulosa* and *Valanga irregularis*, but these studies have not included estimates of metabolic rate. Additionally, there is little published work on the metabolism of grasshoppers in the Austalian Wet Tropics in general, let alone for specific species. As abundant organisms in an area of high ecological importance, this is a noticeable gap. A future avenue of potential research would be to collect data on more grasshopper species of the Australian Wet Tropics. While only four species were analysed in this study, more species were encountered; however, time constraints prevented us from investigating them in detail. Future studies involving larger samples sizes of other Australian tropical species would be useful for better understanding the metabolism of invertebrate species of the Australian Wet Tropics. Additionally, future study should fast specimens prior to metabolic measurements to generate data directly comparable to data from other species from other parts of the world.

Conclusions

Grasshoppers from the Australian Wet Tropics have a power relation between mass and metabolism of 0.97, which is higher than the 0.75 predicted by Kleiber's Law. There is no significant difference in metabolic efficiency (the metabolic rate/mass) between *Austacris guttulosa* and *Valanga irregularis*.

Acknowledgements

Thank you to the staff at the Daintree Rainforest Observatory for their assistance.

References

Chown SL, Marais E, Terblanche JS, Klok CJ, Lighton JRB, Blackburn TM (2007) Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Functional Ecology* **21,** 282–290. doi.org/10.1111/j.1365-2435.2007.01245.x

Fielding DJ, Defoliart LS (2008) Relationship of metabolic rate to body size in Orthoptera. *Journal of Orthoptera Research* **17,** 301–306. doi.org/10.1665/1082-6467-17.2.301

Greenlee KJ, Harrison JF (2004) Development of respiratory function in the American locust *Schistocerca americana*; I. Across-instar effects. *Journal of Experimental Biology* **207,** 497. doi.org/10.1242/jeb.00767

Groenewald B, Chown SL, Terblanche JS (2014) A hierarchy of factors influence discontinuous gas exchange in the grasshopper *Paracinema tricolor* (Orthoptera: Acrididae). *Journal of Experimental Biology* **217,** 3407–3415. doi.org/10.1242/jeb.102814

Hawlena D, Schmitz OJ (2010) Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences of the United States of America* **107,** 15503–15507. doi.org/10.1073/pnas.1009300107

John B, King M (1983) Population cytogenetics of *Atractomorpha similis*. *Chromosoma* **88,** 57–68. doi.org/10.1007/BF00329504

Milner RJ, Staples JA, Prior C (1996) Laboratory susceptibility of *Locusta migratoria* (L.), *Austracrisguttulosa* (Walker) and *Valanga irregularis* (Walker) (Orthoptera: Acrididae) to an oil formulation of *Metarhizium flavoviride* Gams and Rozsypal (Deuteromycotina: Hyphomycetes). *Australian Journal of Entomology* **35,** 355–360. doi.org/10.1111/j.1440-6055.1996.tb01418.x

Murray DAH, Clarke MB, Ronning DA (2013) Estimating invertebrate pest losses in six major Australian grain crops. *Australian Journal of Entomology* **52,** 227–241. doi.org/10.1111/aen.12017

Niklas KJ, Kutschera U (2015) Kleiber's Law: How the *Fire of Life* ignited debate, fueled theory, and neglected plants as model organisms. *Plant Signaling & Behavior* **10,** e1036216. doi.org/10.1080/15592324.2015.1036216

Sousa T, Domingos T, Kooijman SALM (2008) From empirical patterns to theory: a formal metabolic theory of life. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363,** 2453–2464. doi.org/10.1098/rstb.2007.2230

Trisnawati DW, Tsukamoto T, Yasuda H (2015) Indirect effects of nutrients in organic and conventional paddy field soils on the rice grasshopper, *Oxya japonica* (Orthoptera: Acrididae), mediated by rice plant nutrients. *Applied Entomology and Zoology* **50,** 99–107. doi.org/10.1007/s13355-014-0309-4