

Effects of temperature on locomotion rate of the introduced slug *Deroceras panormitanum* (Gastropoda: Limacidae) on Marion Island: Impacts of global climate change

Natasha P. Mothapo

Centre for Invasion Biology, Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland, 7602

E-mail: **13707930@sun.ac.za**

Abstract

Many of the Southern Ocean Islands are experiencing rapid climate change. These islands have been invaded by a wide variety of species, which are having substantial effects on ecosystem functioning. Temperatures have increased by *c.* 1.2°C and rainfall has declined by 500 mm in the past half century on Marion Island. The slug, *Deroceras panormitanum* is an important invasive on Marion Island. Its distribution is largely restricted to moist, lowland areas below 200 m a. s. l. What the influence of temperature is on other aspects of performance that might be significant in determining the range limits of this species, such as locomotion ability, is not known. The primary aim of this study was to determine the effects of temperature on locomotion performance by investigating three aspects of performance curves: optimum temperature (T_{opt}), performance breadth (T_{br}) and maximum velocity (U_{max}). The responses of optimum temperature and performance breadth showed reverse acclimation. Individuals acclimated to the colder temperature (0°C) showed a higher optimum temperature and a wider performance breadth over all the groups. Field fresh individuals performed poorly overall. There were no significant acclimation effects on maximum velocity (U_{max}). The slugs seem to prefer temperatures between 5°C and 10°C, even though they perform poorly at these temperatures. If temperatures increase as predicted for the Southern Ocean Islands, slugs are likely to have increasing impacts on ecosystem functioning.

Introduction

Two major changes being wrought on biota globally are climate change and biological invasions. Climate change is likely to change the distribution and abundance of many species. For example, Warren et al. (2001) demonstrated that British non-migratory butterflies have increased their distribution and abundances in response to warming associated with global climate change. Indeed, it has been suggested that many assemblages will be wholly rearranged with modern climate change (Walther et al. 2002), as has taken place in the past in response to variation in the planet's climate (Dynesius and Jansson 2000). Biological invasions are also altering ecosystem structure and functioning by adding species in many systems, and by causing the extinctions of others (Sax and Gaines 2003; Blackburn et al. 2004). It is widely thought that interactions between climate change and biological invasions will interact synergistically to enhance the rate of change of assemblages and ecosystems (Dukes and Mooney 1999).

This is true also for the Southern Ocean Islands. Many of these islands are experiencing rapid climate change. For example, at Marion Island temperature has increased by *c.* 1.2°C and total annual precipitation declined by 500 mm in the past 50 years (Smith 2002). Likewise, the islands have been invaded by a wide variety of species, many of which are having substantial effects on ecosystem structure and functioning (e.g. Smith and Steenkamp 1990; Hänel and Chown 1998; Huyser et al. 2000). Recent studies have revealed increases in the abundances of established alien species and in the strength of their negative impacts of local biota, especially through indirect interactions (Bergstrom and Chown 1999). For example, the house mouse, *Mus musculus* L., has had a substantial impact on invertebrates and plants at Marion

Island since its introduction (Chown and Smith 1993; Smith et al. 2002). It is thought to be responsible for significant alterations to terrestrial ecosystems on several Southern Ocean Islands (Le Roux et al. 2002; Smith et al. 2002; Jones et al. 2003).

Interactions between climate change and the impacts of invasive species are also likely to be significant. It has been suggested that climate change will favour introduced species in the sub-Antarctic owing to their poor tolerance of cold (Walther et al. 2002). Typically, alien species have low richness on cold islands (Chown et al. 1998), and on particular islands (such as Marion Island Gough Island) are usually restricted to warmer, low-lying areas (Gabriel et al. 2001; Jones et al. 2003). Moreover, the warming and drying trend that is now being recorded on many of the Southern Ocean Islands (Chown et al. 2002; Smith 2002; Frenot et al. 2004) is likely to favour introduced invertebrates over indigenous ones for several reasons. First, it is clear that invasive species tend to be less tolerant of low temperature stress than are indigenous species. Thus, increasing temperatures will enable invasive species to increase their ranges, often at the expense of indigenous species (see Convey et al. 1999; Jones et al. 2003). Second, indigenous species tend to have long life cycles (Barendse and Chown 2000; Chown et al. 2002). In addition, it appears that indigenous species have a shallower rate-temperature response than invasive ones. In consequence, increases in temperature are likely to mean even faster life cycles for invasive species, and this might mean eventual domination of ecosystems by them (Chown et al. 2002). Finally, increasing temperatures might improve performance by shifting mean environmental conditions into the performance optimum of the species concerned, so enabling faster growth and higher eventual rates of increase.

The slug, *Deroceras panormitanum* is an important invasive species on Marion Island. It was first recorded on the island in 1972, and it is thought to have been introduced to the island in the 1960's from the Western Cape region of South Africa (Smith 1992). On the island, the species prefers lowland areas and it is commonly found in drainage line communities dominated by *Acaena magellanica* and *Brachytheceium rutabulum* (Smith 1992). The slug is also abundant in biotically influenced coastal sites among swards of *Poa cookii* and *Poa annua*. However, it is thought that the species is unable to traverse the high, cold grey lava ridges such as Long Ridge and Stony Ridge, and that this might limit its distribution. Nonetheless, it is found around Marion Island, and Smith (2002) attributed the circum-island distribution to transport by helicopter. Individual slugs are commonly found hiding beneath structures placed on the ground. They may, therefore, have hitchhiked their way around the island on supplies often stored on the ground at the scientific station and then airlifted to field huts around the island.

The species has considerable impacts on the local ecosystem. Smith and Steenkamp (1992) showed that moth larvae, earthworms, weevil larvae and adults, snails and slugs enhanced nutrient release in their microcosm experiment. Of these species, *Deroceras panormitanum* had the greatest influence on nutrient release of all the invertebrates examined, except perhaps for *Pringleophaga marioni* (Smith and Steenkamp 1992). *Deroceras panormitanum*, significantly enhanced rates of nutrient release in 78% of the litter/nutrient combinations tested. The slug is presently probably having significant impacts on the island ecosystem (especially since it has no predators (Smith 2002)) and if it increases its distribution as the island's climate changes, it might have further impacts.

Whether or not *D. panormitanum* will increase its distribution depends on what limits its range. Smith (1992) suggested that low temperatures limit the range of the slug. Goldberg (2004) found that the slugs tend to be abundant below 200 m above sea level and are cold intolerant. They freeze at c. -0.3°C , which is slightly higher than soil surface temperatures above 200 m. Moreover, Goldberg (2004) also found that slugs are intolerant of saline conditions, which may explain their slow progress in spreading past the cliffs that lie at the seaward limit of some high, grey lava areas (i.e. Triegaardt Bay, Crawford Bay). However, what the influence of temperature is on other aspects of performance that might be significant in determining the range limits of this species, such as locomotion ability (see Gilchrist 1996; Angiletta et al. 2002), is not known for this species.

The extent of phenotypic plasticity in this species, which might enable it to better respond to climate change than otherwise might have been the case (see Davis and Shaw 2001; Helmuth et al. 2005), is also poorly known. Phenotypic plasticity is defined as the malleability of an organism's phenotype in response to environmental conditions experienced or anticipated by that organism (Huey and Berrigan 1996). It is often thought that acclimation will enhance performance and must thus be adaptive (Huey and Berrigan 1996; Bennett and Lenski 1997; Chown and Nicolson 2004; Deere and Chown *submitted manuscript*). Several responses to acclimation can be expected. These responses are physiological examples of phenotypic plasticity (Huey and Berrigan 1996). The Beneficial Acclimation Hypothesis (BAH) states that acclimation to a particular environment gives an organism a performance advantage in an environment over another organism that has not had the opportunity to acclimate

to that particular environment (Leroi et al. 1994). Much of the recent literature suggests that despite the seemingly obvious benefits of acclimation, there is little or poor support for it (Huey and Berrigan 1996; Bennett and Lenski 1997; Huey et al. 1999; Gibert et al. 2001; Woods and Harrison 2001; Deere and Chown *submitted manuscript*). However, several responses to acclimation can be expected and many of the alternative hypotheses of the BAH appear more plausible (Huey and Berrigan 1996). The “Colder Is Better” (CIB) hypothesis predicts that individuals raised at low temperatures will perform better in any thermal environment than organisms raised at higher temperatures. The “Hotter Is Better” (HIB) hypothesis is a counterpoint to the Colder Is Better hypothesis (Huey et al. 1999). The Deleterious Acclimation Hypothesis (DAH) predicts that detrimental effects of extreme conditions will have negative consequences for the organism (Huey and Berrigan 1996). However, performance in one environment may sometimes be enhanced by acclimating to a different environment (Huey et al. 1999).

Therefore, the primary aim of this study is to determine the effects of temperature on the locomotion performance of *D. panormitanum* and the extent of phenotypic plasticity in this species, by investigating the response to acclimation of three aspects of thermal performance curves: Optimum temperature, optimum speed and performance breadth (Gilchrist 1996). Locomotion performance was chosen as a trait because it is directly linked to fitness in a wide variety of organisms (Gilchrist 1996; Gibert et al. 2001; Marvin 2003; Wilson and Johnson 2004). In testing the response of this trait to acclimation, the predictions of the major acclimation hypotheses are also examined.

Materials and Methods

Study site and study animal

This study was conducted on Marion Island during the annual relief voyage in April 2005. Marion Island (47°54'S 37°45'S) is a sub-Antarctic Island (Smith 2002) situated just north of the Antarctic Polar Frontal Zone (APFZ), at a distance of 2300 km SE of Cape Town (Smith 1987). It is the larger of the two islands forming the Prince Edward Island group. Temperatures on the island are relatively low, with a mean annual temperature of 5°C (Smith 2002). The island has an oceanic climate characterized by strong westerly winds, high precipitation and high humidity (Smith 2002). The climate is thermally stable (Hänel and Chown 1998), although soil surface temperatures may drop below zero during any month of the year (Sinclair and Chown 2003). Temperatures have been increasing on the island in step with global climate change, and mean annual temperature has increased by 1.2°C over the past half century, while total annual precipitation has declined by more than 500 mm over the same period (Smith 2002).

Slugs were hand collected at Trypot Beach from the grasses *Poa cookii* and *Poa annua*, and the forb *Cotula plumosa* (Asteraceae) and placed in plastic containers (375 ml) with perforated lids. Samples of the vegetation were included in the collection containers to maintain humidity and to provide a food source. A maximum of 20 individuals was kept in each 375 ml plastic container during sampling. The slug's distribution is largely restricted to moist, lowland areas of the east coast (below c. 200 m a. s. l) (Goldberg 2004).

Experimental design

Thirty animals were acclimated to each of four acclimation temperatures (0°C, 5°C, 10°C, 15°C) in regulated climate chambers, with a day light cycle of 12L: 12D. Each animal was kept individually in a 40 ml plastic vial with a piece of *Cotula plumosa* leaf and a small drop of water. The animals were kept in climate chambers for seven days, as it is the appropriate acclimation time for many species (e.g. Klok and Chown 2003; Deere and Chown, *submitted manuscript*), and food was replaced every second day. Animals were randomised and rotated between the shelves daily, during the acclimation period, to prevent potential within-chamber acclimation effects or shelf effects. The same procedure was used for field fresh animals. However, the field fresh animals were kept under ambient conditions outside the laboratory, for a maximum of 13 hours, until experimentation.

Testing locomotor performance

Animals were placed on a temperature controlled walking stage (50 cm X 50 cm) attached to a Grant LTD 20 (Grant Instruments, Cambridge, UK) waterbath. A Type T copper-constantan thermocouple (40 SWG) was attached to the surface of the walking stage to ensure the correct temperature was held.

A pilot study was conducted prior to experimentation to determine thermal equilibration times of individual slugs on the walking stage. Two tests were conducted with ten animals per test. In the first test the slugs were kept at 0°C for one day in a climate chamber and then placed directly onto the warm surface of the walking stage, that was regulated at 45°C ($\pm 1^\circ\text{C}$). In the second assessment, slugs were kept at 15°C and then placed directly on to the cold surface of the walking stage

that was regulated at 0°C (\pm 1°C). These treatments were selected because they represent the most extreme experimental treatments that were used in this study. Each individual was placed in the finger of a latex glove with a Type T copper-constantan thermocouple (40 SWG) attached to a digital thermometer. A second thermocouple was attached directly to the surface of the walking stage to ensure the correct temperature was held. The slug, with the thermocouple, was placed directly on the surface of the walking stage and allowed to equilibrate. Five minutes was selected as the equilibration time because this was considered to encompass the majority of the possible maximum equilibration times (see Table 1).

In the main trials, four individuals were placed directly on the surface of the walking stage and allowed to equilibrate. Animals were taken directly from the climate chamber and returned immediately after each test. Each individual was then tested separately, while the others remained on the walking stage. The distance the animal covered within 20 s was measured. This was repeated three times per individual and the maximum distance travelled in 20 s was selected. The individuals were first allowed to crawl around and measurements were started only when they had been moving consistently for more than five seconds. Data from individuals that stopped or faltered during experimentation was discarded. The distance covered by each individual was determined from -5°C to 20°C at every 5°C increment. Animals were kept in the climate chamber while the waterbath was altered to the next test temperature. Test temperatures were not randomised. The weight of each individual was determined using an Avery Berkel (FA304T, EU) electronic microbalance (accuracy of 0.1 mg), before the start of the replicates and at the end of the three

replicates at each test temperature. A sample size of twelve animals was used at field fresh and at each acclimation temperature.

Performance curves were constructed using locomotion data and the following key traits were calculated according to Gilchrist's (1996) formula. Performance breadth (T_{br}) – index of breadth of the curve; optimum temperature (T_{opt}) – the thermal conditions that maximise performance; and maximum speed (U_{max}) – the maximum rate of performance, or the optimum speed at T_{opt} . T_{opt} and U_{max} were obtained from the experimental data (performance curves) and were used to calculate T_{br} using Gilchrist's (1996) formula:

$$T_{br} = \sqrt{\sum \left[\frac{u_i (T_i - T_{opt})}{u_{max}} \right]^2}$$

The effects of acclimation treatments on each of the traits (T_{opt} , T_{br} and U_{max}) was assessed by inspecting the performance curves and by formally assessing the effects of acclimation temperatures on each of the traits using a Generalized Linear Model (GLZ) assuming a normal distribution of errors with a log link function, based on individual data points.

Results

Slug body temperatures had usually equilibrated within five minutes on the stage, and performance curves displayed the conventional unimodal curve (Table 1), indicating that this was sufficient to ensure that no artefacts were generated by mismatches between slug temperature and stage temperature. Performance curves were typically

unimodal, as usually found to be the case (Fig. 1). T_{opt} varied significantly, but inconsistently with acclimation treatment, with the highest value being recorded at the lowest acclimation temperature and the lowest value in the field fresh group (Table 2). Performance breadth showed the same pattern (Table 2), suggesting that acclimation to low temperatures has a different effect to the other treatments. By contrast, U_{max} showed no variation with acclimation temperature, and only the field fresh individuals had a mean U_{max} slightly lower than those of the individuals subjected to acclimation treatments (Table 1). The differences in the acclimation treatments in T_{opt} and T_{br} , and the absence of difference in U_{max} remained when data from field fresh individuals were excluded from the analysis (Table 2). The typically higher values for locomotion speed in the 0°C acclimated individuals at test temperatures beyond the optimum are readily discernable from the performance curves (Fig. 1)

Discussion

The Beneficial Acclimation Hypothesis (BAH) predicts that organisms acclimated to a particular temperature should be significantly more fit at that temperature than organisms acclimated to some other temperature (Leroi et al. 1994). Much of the recent literature suggests that despite the seemingly obvious benefits of acclimation, there is very little support or poor support for it (Bennett and Lenski 1997; Deere and Chown *submitted manuscript*; Gibert et al. 2001; Huey and Berrigan 1996; Huey et al. 1999; Woods and Harrison 2001). The results from this study do not support the BAH. None of the acclimated groups performed better at the temperatures that they were acclimated to (Fig. 1) and in fact the converse was observed. The response of performance breadth (T_{br}) and optimum temperature (T_{opt}) show inverse acclimation, which is the opposite of what is expected after beneficial acclimation. The values for

both performance breadth and optimum temperature decrease with increasing acclimation temperatures. The colder acclimation resulted in a higher optimum temperature and a wider performance breadth. Optimum temperature at 15°C acclimation is slightly higher than it was at 10°C acclimation, and this could be a result of stress.

Wilson and Franklin (2000) demonstrated that in adults of the striped marsh frog, *Lymnodynastes peronii*, locomotor performance does not respond to different acclimation temperatures. Therefore, the frogs show no acclimation, or are incapable thereof. This is one of the alternative responses to beneficial acclimation. Gibert et al. (2001) demonstrated that walking speeds of *Drosophila melanogaster* (raised at low temperatures) increased with age and test temperatures compared to flies raised at a high temperature. This result supports the optimum development temperature hypothesis (Huey and Berrigan 1996), an alternative hypothesis of the BAH that predicts that individuals raised at intermediate temperatures will be more vigorous at all temperatures (Huey and Berrigan 1996). Maximum velocity for *D. panormitanum* did not show a significant response to acclimation, while performance breadth and optimum temperature showed a small reverse response. Thus, *D. panormitanum* either shows no plasticity or an inverse acclimation response as a consequence possible of low temperature stress. The result of acclimation is in keeping with several studies both from elsewhere and from Marion Island. Thus, Kaufmann and Bennet (1989) showed that acclimation did not affect the sprint speed or performance of the lizard, *Xantusia vigilis*, and Wilson and Franklin (2000) found a similar effect for a frog species. Deere and Chown (*submitted manuscript*) conducted a similar study on five mite species from Marion Island. They found no plasticity (i.e. no response to

acclimation) and attributed their finding to the short-term unpredictability of the climate on Marion Island. Those similar results were found here for *D. panormitanum* raises the interesting possibility that acclimation effects might evolve very quickly, though of course, the slugs might already have had such a response prior to their arrival at the island. Only a comparison of the Marion Island population with one from the Western Cape, the putative source pool, would demonstrate which of the hypotheses could be rejected.

The difference of U_{\max} between the field and laboratory could be a result of favourable conditions in the laboratory. There is only a slight difference between the values of all the acclimation groups, which are slightly higher than the field fresh group. To avoid cold, many ectothermic species migrate into buffered habitats, maintaining a high level of humidity and avoiding extreme temperature (Ansart and Vernon 2003). Many of the slugs were found cushioned between the roots and leaves of *Cotula plumosa* and the grass *Poa cookii*. Microclimate temperature may also have an effect on the acclimation response of the slug. The poor performance of the field fresh could be a reaction to possible stress due to handling.

Variation in locomotor performance or thermal sensitivity may indicate fitness differences (Gilchrist 1996). Marshall and Chown (1995) showed that locomotor activity rates of two oribatid mites from the sub-Antarctic increased with temperatures above zero, but walking was severely impaired at temperatures below freezing. The same can be observed for the slugs (Fig. 2). All the groups performed poorly at -5°C . That they performed at all given the record of freezing at -0.3°C by Goldberg (2004) is surprising. This is likely to be due to variation in the conditions to which the slugs

were exposed, especially because Goldberg (2004) kept the slugs moist at all times, which is likely to have elevated the temperatures of inoculative freezing.

The two main factors that are important to determine how a species population will respond to climate change is the flexibility or phenotypic plasticity of that species, and the rate of evolution (Berteaux et al. 2004). If a species shows poor response to short and long term changes, then the general fitness will decrease with climate change (Berteaux et al. 2004). The results for optimum temperature show that the slugs prefer temperatures between 5°C and 10°C (Table 2). The field fresh individuals have a similar optimum temperature to 10°C and 15°C. These might be the daily temperatures they experience in their microhabitats. The main trait that is investigated here, in the context of phenotypic flexibility, is maximum velocity. The results show that this trait is not flexible for this species. Maximum velocity did not show a significant response to acclimation (Table 2).

It is difficult to predict climate change in the slug's context. *Deroceras panormitanum*'s distribution is restricted to the lowland areas below 200 m a.s.l. Temperatures at higher altitudes are cooler and the areas are drier above the 200 m a.s.l mark. Goldberg (2004) predicted that a warmer environment, as a result of climate change, would allow the slugs cross the 400 m a. s. l mark, thereby increasing their ranges. The present results suggest that slugs are capable of locomotor performance across a reasonably broad range of temperatures, (performance breadth varies between 8°C and 14°C), and should therefore have no difficulty in taking advantage of elevated temperatures from a locomotion perspective. Therefore, if temperatures keep increasing, as predicted for climate change on Marion Island, the

slugs will be able to colonize a wider range of areas and show elevated performance in the areas they currently occupy. Thus, the impact of the slugs on the terrestrial system is likely to increase with increasing climate change, as Smith (2002) predicted.

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References

- Angilletta M J, Niewiarowski PH, Navas CA (2002). The evolution of thermal physiology in ectotherms. *J Therm Biol* 27: 249-268.
- Ansart A, Vernon P (2003) Cold hardiness in molluscs. *Acta Oecologia* 24: 95-102
- Barendse J, Chown SL (2000) The biology of *Bothrometopus elongatus* (Coleoptera, Curculionidae) in a mid-altitude fellfield on sub-Antarctic Marion Island. *Polar Biol* 23: 346-351.
- Bennett AF, Lenski RE (1997) Evolutionary adaptation to temperature. VI. Phenotypic acclimation and its evolution in *Eschericia coli*. *Evolution* 51: 36-44
- Bergstrom DM, Chown SL (1999) Life at the front: history, ecology and change on southern ocean islands. *Trends Ecol Evol* 14: 473-477
- Berteaux D, Réale D, McAdam AG, Boutin S (2004) Keeping pace with fast climate change: can arctic life count on evolution. *Integr Comp Biol* 44: 140-151

- Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston, K.J (2004) Avian extinction and mammalian introductions on oceanic islands. *Science* 305: 1955-1958.
- Chown SL, Gremmen NJM, Gaston KJ (1998) Ecological biogeography of Southern Ocean Islands: species-area relationships, human impacts, and conservation. *Am Nat* 152: 562-575
- Chown SL, McGeoch MA, Marshall DJ (2002) Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *Afric Entomol* 10: 67-82
- Chown SL, Nicolson SW (2004). *Insect Physiological Ecology. Mechanisms and Patterns*. Oxford University Press, Oxford.
- Chown SL, Smith VR (1993) Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* 96: 508-516
- Convey P, Greenslade P, Arnold RJ, Block W (1999) Collembola of sub-Antarctic South Georgia. *Polar Biol* 22: 1-6.
- Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. *Science* 292: 673-679.
- Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends Ecol Evol* 14: 135-139
- Dynesius M, Jansson R (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the U.S.A.* 97: 9115-9120.

- Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicki M, Bergstrom D.M (2004) Biological invasions in the Antarctic: extent, impacts and implications. *Biol Rev* 79: 1-28
- Helmuth B, Harley CDG, Halpin P.M, O'Donnell M, Hofmann GE, Blanchette CA (2002). Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298: 1015-1017.
- Huey RB, Berrigan D (1996). Testing evolutionary hypotheses of acclimation. Pp. 205-237 in I. A. Johnston and A. F. Bennett, Eds. *Animals and Temperature. Phenotypic and Evolutionary Adaptation*. Cambridge University Press, Cambridge.
- Gabriel AGA, Chown SL, Barendse J, Marshall DJ, Mercer RD, Pugh PJA, Smith V R (2001). Biological invasions of Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* 24: 421-430.
- Gibert P, Huey RB, Gilchrist GW (2001) Locomotor performance of *Drosophila melanogaster*: Interactions among developmental and adult temperatures, age, and geography. *Evolution*. 55: 205-209
- Gilchrist GW (1996) A quantitative genetic analysis of thermal sensitivity in the locomotor performance curve of *Aphidius ervi*. *Evolution* 50: 1560-1572
- Goldberg S (2004) Factors influencing the distribution of an alien invasive slug *Deroceras caruanae* (Gastropoda: Limacidae) on Marion Island. Honours Thesis. University of Stellenbosch
- Hänel C, Chown SL (1998) An introductory guide to Marion and Prince Edward Island Special Nature Reserves, 50 years after annexation. Published by the department of environmental affairs and tourism, Pretoria

- Hänel C & Chown SL (1998) The impact of a small, alien invertebrate on a sub-Antarctic terrestrial ecosystem: *Limnophyes minimus* (Diptera, Chironomidae) at Marion Island. *Polar Biol* 20: 99-106
- Huey RB, Berrigan D, Gilchrist GW, Herron JC (1999). Testing the adaptive significance of acclimation: A strong inference approach. *Am Zool* 39: 323-336.
- Huysen O, Ryan PG, Cooper J (2000) Changes in population size, habitat use and breeding of the lesser sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? *Biol Conserv* 92: 299-310.
- Jones AG, Chown SL, Ryan PG, Gremmen NJM, Gaston KJ (2003) A review of conservation threats on Gough Island: a case study for terrestrial conservation in the Southern Oceans. *Biol Conserv* 113: 75-87.
- Kaufmann JS, Bennett AF (1989) The effect of temperature and thermal acclimation on locomotor performance in *Xantusia vigilis*, the desert night lizard. *Physiological Zoology* 62: 1047-1058.
- Klok CJ, Chown SL (2003) Resistance to temperature extremes in sub-Antarctic weevils: interspecific variation, population differentiation and acclimation. *Biol J Linn Soc* 78: 401-414.
- Le Roux V, Chapuis JL, Frenot Y, Vernon P (2002) Diet of the house mouse (*Mus musculus*) on Guillou Island, Kerguelen archipelago, Subantarctic. *Polar Biol* 25: 49-57
- Marshall DJ, Chown SL (1995) Temperature effects on locomotor activity rates of sub-Antarctic oribatid mites. *Polar Biol* 15: 47-49
- Marvin GA (2003) Effects of acute temperature and thermal acclimation on aquatic and terrestrial locomotor performance of the three-lined salamander, *Eurycea guttolineata*. *J Therm Biol* 28: 251-259

- McCarty JP (2001) Ecological consequences of recent climate change. *Conserv Biol* 15: 320-331
- Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. *Bull Amer Meteor Soc* 81: 443-450
- Sax, D.F. & Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends Ecol Evol* 18: 561-566.
- Sinclair BJ, Chown SL (2003) Rapid responses to high temperature and desiccation but not to low temperature in the freeze tolerant sub-Antarctic caterpillar *Pringleophaga marioni* (Lepidoptera, Tineidae). *J Insect Physiol* 49: 45-52.
- Slabber S, Chown SL (2002) The first record of a terrestrial crustacean, *Porcellio scaber* (Isopoda, Porcellionidae), from sub-Antarctic Marion Island. *Polar Biol* 25: 855–858
- Smith VR, Steenkamp M (1990) Climate change and its ecological implications at a sub-Antarctic island. *Oecologia* 85: 14-24
- Smith VR, Steenkamp M (1992) Macroinvertebrates and litter nutrient release on a sub-Antarctic Island. *S Afric J Bot* 58: 105-116
- Smith VR (1987) The environment and biota of Marion Island. *S Afric J Science* 83: 211-220
- Smith VR (1992) Terrestrial slug recorded from sub-Antarctic Marion Island. *J Mollusc Stud* 58: 50-81
- Smith VR (2002) Climate change in the sub-Antarctic: An illustration from Marion Island. *Climate Change* 52: 345-357
- Smith VR, Avenant NL, Chown SL (2002) The diet and impact of house mice on a sub-Antarctic island. *Polar Biol* 25: 703–715.

- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416: 389-395.
- Warren MS, Thomas, JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-68
- Wilson RS, Franklin CE (2000) Inability of adult *Limnodynastes peronii* (Amphibia: Anura) to thermally acclimate locomotor performance. *Comp Biochem Physiol A* 127: 21-28
- Wilson RS, Johnston IA (2004) Combining studies of comparative physiology and behavioural ecology to test the adaptive benefits of thermal acclimation. *International Congress Series* 1275: 201-208
- Woods HA, Harrison JF (2001) The Beneficial acclimation Hypothesis versus Acclimation of specific traits: Physiological change in water- stressed *Manduca Sexta* caterpillars. *Physiol Biochem Zool* 74: 32-44.

Figure Legends

Figure 1 Performance curves with mean (\pm S.E) locomotion speed at each of several test temperatures for field fresh (FF) slugs and for the slugs held at each of the four experimental acclimation temperatures (FF (\square), 0°C (\bullet), 5°C (\blacktriangle), 10°C (\blacksquare), 15°C (\blacklozenge)).

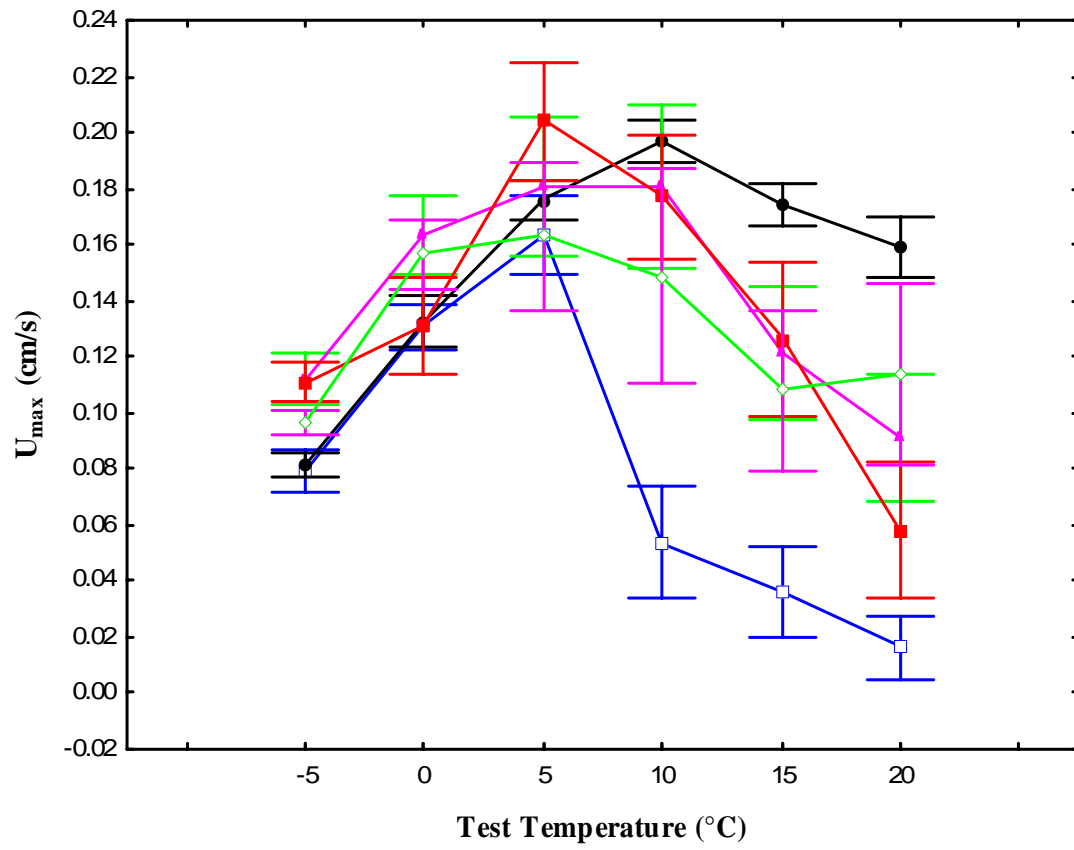


Figure 1

Table 1 Equilibration times for slugs acclimated at 0°C for 24 hours and exposed to 45°C, and slugs acclimated at 15°C for 24 hours and exposed to 0°C; Mean (\pm S.E), Minimum (Min) and Maximum (Max) are reported. These represent the extreme cases of equilibration from cold acclimation temperature to warm test temperature and from warm acclimation temperature to cold test temperature.

| Acclimation (°C) | Mean\pm S.E | Minimum | Maximum |
|-------------------------|---------------------------------|----------------|----------------|
| 0 | 2.06 \pm 0.394 | 0.55 | 4.36 |
| 15 | 3.51 \pm 0.438 | 1.16 | 5.32 |

Table 2 Mean (\pm S.E) optimum temperature (T_{opt}), mean (\pm S.E) performance breadth (T_{br}) and mean (\pm S.E) maximum velocity (U_{max}) for *Deroceras panormitanum* individuals at the different acclimation temperatures. Superscript letters indicate significant differences between acclimation temperatures on 95% confidence intervals following a Generalized Linear Model (GLZ). A normal distribution of errors with log link function was selected for all three traits T_{br} , T_{opt} and U_{max} .

| Acclimation ($^{\circ}$ C) | T_{opt} ($^{\circ}$ C) ¹ | Minimum | Maximum | T_{br} ($^{\circ}$ C) ² | Minimum | Maximum | U_{max} (cm/s) ³ | Minimum | Maximum | N |
|-----------------------------|--|---------|---------|---------------------------------------|---------|---------|-------------------------------|---------|---------|----|
| FF | 4.09 ± 1.26^A | 0 | 15 | 7.77 ± 1.16^A | 5.25 | 18.95 | 0.17 ± 0.01^A | 0.11 | 0.25 | 11 |
| 0 $^{\circ}$ C | 10.00 ± 0.87^B | 5 | 15 | 13.57 ± 0.63^B | 10.75 | 17.51 | 0.21 ± 0.01^B | 0.18 | 0.24 | 12 |
| 5 $^{\circ}$ C | 6.67 ± 0.94^C | 0 | 10 | 11.12 ± 1.05^C | 3.59 | 17.86 | 0.23 ± 0.02^B | 0.12 | 0.33 | 12 |
| 10 $^{\circ}$ C | 5.42 ± 1.14^{AC} | -5 | 10 | 9.72 ± 1.17^{AC} | 0 | 14.26 | 0.23 ± 0.01^B | 0.15 | 0.31 | 12 |
| 15 $^{\circ}$ C | 6.67 ± 1.67^{AC} | 0 | 20 | 9.75 ± 1.55^{AC} | 2.17 | 16.62 | 0.23 ± 0.02^B | 0.15 | 0.3 | 12 |

With FF

1 T_{opt} $X^2_{(4)} = 17.935$, $p < 0.05$

2 T_{br} $X^2_{(4)} = 15.419$, $p < 0.05$

3 U_{max} $X^2_{(4)} = 12.621$, $p < 0.05$

Without FF

1 T_{opt} $X^2_{(3)} = 9.342$, $p < 0.05$

2 T_{br} $X^2_{(3)} = 8.592$, $p < 0.05$

3 U_{max} $X^2_{(3)} = 2.282$, $p > 0.05$

