The effects of rainfall unpredictability on the circadian energy rhythms of the four-striped field mouse, *Rhabdomys pumilio.*

Stephanie Johnson

Dept. of Zoology & Entomology
University of Natal
Private Bag X01
Scottsville
3209
South Africa

Preface

The experimental work described in this dissertation was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from January 1996 to January 1998, under the supervision of Dr Barry Lovegrove.

These studies represent original work by the author and have not been submitted in any form for any degree or diploma to any University. Where use has been made of work of others, it is duly acknowledged in the text.

Acknowledgements

Summary

Rainfall is the most important factor limiting primary production, and hence food availability, in ecosystems. This study tests the thesis that, under conditions where rainfall is unpredictable and food supply varies spatially and temporally from year-to-year, physiological energy-saving mechanisms should evolve in animals for which migration is not an option to avoid periods of low habitat productivity. Apart from the normally erratic rainfall patterns characteristic of arid regions, unpredictable seasonal rainfall may also occur in mesic zones as a consequence of climatic phenomena such as the El Niño Southern Oscillations (ENSO). Using two hypothetical models, this study attempts to determine whether the respective evolutionary history of both aridity and ENSO can be detected in the various phenotypic physiological traits of *Rhabdomys pumilio* from across southern Africa. Model 1 predicts that a gradient of conservatism of physiological traits related to metabolism, will be detectable along an aridity gradient. Model 2 predicts an increase in the conservatism of similar traits correlated with both the aridity gradient and the gradient of negative rainfall anomalies that are associated with the ENSO.

Measurements of circadian rhythms of body temperature and oxygen consumption of individuals of *R. pumilio* collected from six sites across southern Africa showed that the geographic variation in the physiological traits and proximate responses of this species was explained better by Model 2 than by Model 1. Furthermore, for some traits and proximate responses of this species it was shown that, although the stresses associated with unpredictable rainfall occur less frequently in non-desert ENSO-zones, they are nevertheless sufficient to mimic the selection pressures of rainfall unpredictability in arid zones.

This study also highlighted the low basal rates of metabolism and the other conservative physiological traits of this species as a whole. The basal metabolic rate of 0.819 $mlO_2/g/h$ and the minimum wet thermal conductance of 0.110 $mlO_2/g/h/°C$ are lower than that predicted by allometry. The circadian amplitude of body temperature of $2.52°C$ and the circadian amplitude of oxygen consumption of 1.39 $mlO_2/g/h$ were higher than those predicted by allometric equations. These deviations from predicted values were attributed to the adaptedness of this species to the physiological energy stresses associated with unpredictable resource availability in southern Africa.

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Introduction

A major focus within vertebrate environmental physiology, comparative physiology and physiological ecology, is the study of adaptation (Garland & Adolph, 1991). Yet, even among contemporary evolutionary biologists, there is no consensus on how best to define adaptation and identify adaptive traits. Reviews by Leigh (1971), Bock (1980), Burian (1983), Wallace, (1984), Brandon (1990) and Baum & Larson (1991) reveal that there are numerous, often conflicting definitions, of adaptation. The operational criteria used to identify phenotypic traits as adaptations, and the principal causal mechanism of adaptation, also remain vague.

The most widely accepted agreement in the study of adaptation is that adaptations are the consequence of natural selection (Krimbas, 1984). Most criticisms of adaptation by natural selection have arisen following teleological arguments which conclude that natural selection moulds traits toward perfection (Mayr, 1988). If these arguments are accepted then the existence of neutral genes and neutral characters would refute natural selection theory. However, as Mayr (1988) explains, since the individual as a whole is the target of selection, many neutral genes with no effect on fitness, will be carried along as "hitch-hikers" of favourable gene combinations. As a result, not every character of an individual or of a species is optimally adapted.

Nevertheless, to avoid these types of confusing arguments, many authors now state that natural selection "results in adaptedness" rather than "produces adaptation" (Mayr, 1988). The term adaptedness is defined by Brandon (1978) and Mills & Beatty (1979) as "the propensity to survive". Mayr (1988) extends this definition and defines adaptedness as "the morphological, physiological and behavioural equipment of a species or a member of a species that permits it to compete successfully with members of its own species or with individuals of another species and that permits it to tolerate the extant physical environment. Improved adaptedness may be due to a particular component of the phenotype, or to a single gene, or to the total genotype."

In light of the term adaptedness, there are two major conventions about the application of the term adaptation (Mayr, 1988). For some authors, an adaptation is any trait that not only increases the adaptedness of its possessor, but that is also the product of evolution by natural selection (Gould & Vrba, 1982; Brandon, 1990; Baum &

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Lauson, 1991). Other authors, in view of documenting the evolutionary history if a trait, define an adaptation as any trait that increases the adaptedness of its possessor, regardless of its history (Bock, 1980; Reeve & Sherman, 1993).

However, most authors agree that any adaptation in an organism is the end product of a long historical sequence of consecutive steps (Mayr, 1988). Since it is not possible to prove the causation of each of these steps, it is almost impossible to prove that adaptations are the direct result of natural selection (Mayr, 1988). Rather, to infer adaptation, the selective value of the specific components of the phenotype must be demonstrated (Mayr, 1988). A program of research intended to elucidate an adaptive significance of differences among individuals, populations or species, is referred to by Gould & Lewontin (1979) as an "adaptionist program".

The term "adaptation" has also been used by physiologists to describe a change that occurs within an individual in response to changes in the environment. Dejours (1987) defines adaptation as "consisting in a change minimizing the physiological strain which results from a stressful environment". These changes are usually nongenetic, generally reversible, and may be attributed to environmental factors such as nutritional status, stress, seasonal variation, environmental effects and maternal effects (Mayr, 1963; Chaffee & Roberts, 1971; Hart, 1971; Hoffman & Parsons, 1989; Parsons, 1991; Garland & Adolph, 1991; Travis, 1992). However, such a capacity for change throughout an individual's life history may itself be genetically based and subject to selection pressures (Gause, 1942; Feder, Bennett, Burggren & Huey, 1987; Burggren & Bemis, 1990; Travis, 1992).

The confusion of the different meanings and uses of the term adaptation have led most evolutionary biologists to emphasize the importance of defining and testing for an adaptation in a manner appropriate for the problem being pursued (Reeve & Sherman, 1993). For the purpose of this study, I use Mayr's (1988) definition of how adaptation is achieved and what criteria should be used to identify an adaptation: "Adaptation is measured by evolutionary success. It is achieved by the greater survival or higher reproductive success of certain individuals owing to the fact that they possess ecological-physiological traits not, or only partially, shared by other individuals of their population. Any trait which increases the ecological-physiological efficiency of an individual and which is useful in the struggle for existence, can be seen as an

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adaptation."

The major difficulty in establishing the adaptedness of characters is methodological (Mayr,1988). Adaptation can only be measured and discussed on a comparative basis (Bradshaw, 1987) and it is usually only possible through correlation to establish the selective value of a given character (Mayr,1988). For example, in this study I will infer adaptation by observing geographical phenotypic variance and correlating this variation with an aspect of the environment that also varies geographically. The foundation of most evolutionary theory rests upon inferences drawn from geographic variation or upon the verification of predictions made about it (Gould & Johnston, 1972). Geographic variation is the smallest amount of evolution that can be detected in nature (Arnold, 1981). Therefore, in the study of adaptation, it is important to observe and quantify geographic variation of traits. Once differences in traits are observed, they may then be related to behavioural and ecological selection.

The study of geographical variation of metabolic traits may provide insight into adaptation since metabolic processes regulate an individual's energy expenditure and hence contribute to the ecological and physiological efficiency of an individual. An animal's metabolic rate can be monitored by measuring circadian rhythms of energy expenditure at different ambient temperatures. Circadian rhythms are a ubiquitous adaptation of eukaryotic organisms to the most reliable and predictable of environmental changes, the 24-hour cycles of light and ambient temperature. Circadian rhythms are cycles around a stable, long term mean (Aschoff, 1982).

Many factors influence the rate of energy expenditure of mammals (McMahon, 1973; McNab, 1980; Hayssen & Lacy, 1985). The variability in mammalian basal metabolic rates has been accounted for mainly on the basis of four ultimate factors; body size (Kleiber, 1932; Brody, 1945; Kleiber, 1961), taxonomy (Hayssen & Lacy, 1985; Nicholl & Thompson, 1987; Dawson, 1989), food habits (McNab, 1970, 1978, 1986, 1988; Scholander et al., 1950; Taylor & Lyman, 1967; Iverson, 1972) and climate (aridity) (Mc Nab and Morrison, 1963; McNab, 1966, Schmidt-Nielsen, 1972; McNab, 1979; Haim, 1984; Lovegrove, 1986; Gorecki et al., 1990; Lovegrove, Heldmaier & Knight, 1991a; Parsons, 1991; Rubal, Choshniak & Haim, 1992; Haim & Izhaki, 1993; Lovegrove, unpub). Proximate factors, such as environmental temperature (Haim, Rubal &Harari, 1993; Weiner & Heldmaier, 1987) and activity (Jansky, 1962; McNab,

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1980), also have a temporary effect on the rate of energy expenditure of the individual.

The study of geographic variation of metabolic traits in animals that are subject to different degrees of abiotic stresses may provide indications of adaptations to stressful environments. Parsons (1991) defines stress as "an environmental factor, usually a physical one - that causes a potentially injurious change in a system". At the metabolic level, stressful conditions normally require the continuous expenditure of excess energy which ultimately becomes incompatible with survival (Parsons, 1991). Stressful conditions including salinity, heavy metals, oxygen deprivation, extremes of heat and cold and desiccation, all pose costs for the maintenance of normal protoplasmic homeostasis and the normal functioning of membranes and enzymes (Parsons, 1991). An organism can increase its tolerance to a wide range of stresses by reducing its metabolic energy requirements to offset the high metabolic cost of physiological stress responses (Parsons, 1991).

Arid environments can be characterised as a stressful environment since animals are subjected to extremes of heat and cold and desiccation (Hadley, 1972; Lovegrove, 1993). Animals in arid environments are therefore continually subjected to energy stress and hence a low BMR would be expected to evolve. Furthermore, arid regions are characterised by erratic rainfall patterns (Liversidge, 1970; Noy-Meir, 1973; Onesta & Verhoef, 1976a, 1976b; Tyson, 1986). Since rainfall is directly correlated with primary production (Noy-Meir, 1973; Hoffman, Barr & Cowling, 1990, Southgate, Masters & Seely, 1996), animals in arid environments experience unpredictable periods of low resource availability. A reduced BMR could be predicted on these grounds since it is considered to represent an adaptation to spatial and temporal heterogeneity in food availability (McNab, 1979). In support of these predictions, several interspecific studies show that desert rodents in general have significantly lower BMR's than mesic rodents (Mc Nab and Morrison, 1963; McNab, 1966, Schmidt-Nielsen, 1972; McNab, 1979; Haim, 1984; Lovegrove, 1986; Gorecki et al., 1990; Lovegrove, Heldmaier & Knight, 1991a; Rubal, Choshniak & Haim, 1992; Haim & Izhaki, 1993). However, there are very few intraspecific comparisons of this kind.

In general, intraspecific geographic variation of BMR in mammalian populations has not been studied very extensively. This lack of information on the intraspecific variability of metabolism is surprising since several authors have emphasized the

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fundamental importance of being able to infer adaptations from even the smallest geographical variations in physiological traits within populations (Gould & Johnson, 1972; Garland & Adolph, 1991). Intraspecific differences are far more readily related to the environment in which the populations occur. The chance that these differences are due to changes in characteristics which occurred in the past and which bear little relation to the population's present environment, is small (Gould & Johnson, 1972). This is always a possibility with interspecific comparisons (Leroi, Rose & Lauder, 1994).

In the few intraspecific comparisons of geographic variation of metabolic traits in rodents, low BMRs have been observed in desert rodents compared with their mesic counterparts (McNab & Morrison, 1963; Nevo & Shkolnik, 1974; Haim & Borut, 1981; Goyal, Ghosh & Prakash, 1981; Haim & Fairall, 1986; Webb & Skinner, 1996). Perhaps the most conclusive study to date was the study of four chromosomal forms of the Israeli mole rat, *Spalax ehrenbergi* (Nevo & Shkolnik, 1974). Oxygen consumption was measured and compared in five populations from different areas. When BMR was correlated with habitat type, it was found that there was a clinal decrease in BMR inversely related to increases in aridity and diploid number. Similarly, deviations from the expected BMR (Kleiber, 1961) increased with increasing aridity.

Lovegrove (1996) has suggested that low metabolic rates appear to be characteristic not only of mammals inhabiting xeric regions, but also of those inhabiting mesic zoogeographical zones influenced by the El Niño Southern Oscillations (ENSO). Apart from the normally erratic rainfall patterns characteristic of arid regions (Liversidge, 1970; Noy-Meir, 1973; Onesta & Verhoef, 1976a, 1976b; Tyson, 1986), unpredictable seasonal rainfall, and hence unpredictable periods of low resource availability, may occur periodically in mesic regions if the local affect of ENSO is a negative rainfall anomaly (Stone *et al.*, 1996). ENSO events are consequences of unpredictable atmospheric perturbations resulting in an eastern displacement of the Walker Circulation and a southern displacement of the Inter-tropical Convergence Zone (ITCZ) (Philander, 1983). Although the southern oscillations cause heatwaves and floods in certain regions such as North and South America, they cause negative rainfall anomalies, or "drought", often for extended periods of time, in the Afrotropical, Australasian and Indomalayan zoogeographical regions (Philander, 1990; Stone *et al.*, 1996). These negative rainfall anomalies result in animals being subjected to unpredictably low habitat productivity,

similar, but on a less frequent scale, to that which occurs in arid regions.

This study attempts to determine whether the respective evolutionary history of aridity and ENSO can be detected in intraspecific, phenotypic traits on a microgeographic scale. My principal hypothesis states that, under conditions where rainfall is unpredictable and food supply varies spatially and temporally from year to year, conservative rates of metabolism should evolve in animals for which migration is not an option to avoid afflicted regions. These conservative rates of metabolism will reduce the energy expenditure of an animal and hence minimise energy stress.

Sources and measures of rainfall unpredictability in southern Africa
Rainfall patterns in arid regions are naturally variable and unpredictable (Liversidge, 1970; Noy-Meir, 1973; Onesta & Verhoef, 1976a, 1976b; Tyson, 1986). An aridity gradient, and hence a gradient of rainfall unpredictability, occurs from west to east across southern Africa. This aridity gradient can be represented by the mean annual rainfall of different regions in southern Africa (Fig. 1), or by the variability of mean annual rainfall across southern Africa (Fig. 2). Arid zones in the western regions of southern Africa are characterised by a low mean annual rainfall that is highly variable from year-to-year.

Mesic zones in the eastern regions of southern Africa are, on the other hand, characterised by a higher mean annual rainfall and less variable rainfall patterns. The co-efficient of variation of mean annual rainfall (CV) is a direct measure of the interannual variabilty, and hence the unpredictability, of rainfall in an area. It is measured as the standard deviation of mean annual rainfall divided by the mean annual rainfall, and is thus inversely related to mean annual rainfall.

The El Niño Southern Oscillations are also a source of unpredictable rainfall patterns in southern Africa. However, the magnitude of ENSO-related negative rainfall anomalies, with respect to the long-term average rainfall pattern, follows a different temporal scale to that pertaining to the desert-related rainfall anomalies. The eastern regions of southern Africa lie in an ENSO-affected zone (Stone *et al.*, 1996) and experience negative rainfall anomalies (drought) during El Niño periods (Figs 3 & 4). El Niño events occur unpredictably every two to ten years and the duration of individual ENSO events varies from several months to a few years (Fig.

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5) (Tyson, 1986; Philander, 1990). Hence, measures of interannual variability of rainfall, such as the co-efficient of variation of mean annual rainfall, will not necessarily reflect ENSO-related rainfall anomalies if they occur less frequently than the "normal" rainfall anomalies in desert regions.

Implications of ENSO-related rainfall unpredictability

The implications of such disparate frequencies of rainfall variability, such as those associated with El Niño, may be important in terms of the evolution of conservative physiological traits in mammals. Although rainfall anomalies, and hence drought-related energy stresses, occur less frequently in ENSO-afflicted zones than they do in desert zones, the magnitude of the stress may be similar. Parsons (1991) has argued that it is the magnitude rather than frequency of stresses associated with aridity, for example, that leads to conservative energetic traits that offset the costs of maintaining homeostasis in desert mammals. Thus, if selection for conservative physiological traits is dependent upon the magnitude, rather than the frequency of stresses, ENSO influences in mesic zones should mimic those prevailing in arid zones.

Comparative energetic traits

Potential physiological traits that could be measured to indicate whether traits have evolved in response to stresses associated with unpredictable rainfall patterns are those which affect the daily energy expenditure (DEE) of the animal. A low DEE ensures that a reduced amount of the energy available to animals is allocated to maintenance requirements. The energy that is "saved" may then be made available for growth and reproduction. Consequently, an animal with a low daily energy expenditure may be expected to optimise its fitness, even during periods of lower productivity. The following are traits which are known to influence the daily energy expenditure of animals.

Basal Metabolic Rate (BMR): In endotherms, metabolism attains a minimum (basal) in the thermoneutral zone (TNZ) (Withers, 1992). Within this range of ambient temperatures, no additional energy is expended to maintain the endotherm's

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body temperature since heat loss to the environment is perfectly balanced by the minimum resting heat production of the animal (Lovegrove et al., 1991b; Withers, 1992). Below the lower critical limit of thermoneutrality (T_{lc}), and at low ambient temperatures (T_a), increased heat production above the BMR compensates for heat loss (Withers, 1992). This represents the only thermoregulatory mechanism open to mammals that do not enter torpor, to maintain homeothermy (McNab & Morrison, 1963; Withers, 1992).

Thermoregulatory heat production comprises the largest component of an endotherm's daily energy budget (Lovegrove et al., 1991b). The ability to maintain an optimal level of metabolism which minimises thermoregulatory costs, but which maintains homeothermy nevertheless, would be advantageous (Lovegrove et al., 1991b). In short, lower-than-expected basal metabolic rates may reduce daily energy requirements.

Minimum wet thermal conductance (C_{min}): Thermal conductance (C) is a measure of the ease with which heat enters or leaves the body (Scholander et al., 1950). It is assumed to attain a minimum (C_{min}) at the lower critical limit of thermoneutrality (Scholander et al., 1950; Aschoff, 1982; Lovegrove et al., 1991b, Withers, 1992). A low thermal conductance, especially in animals from regions subjected to large daily fluctuations in ambient temperatures, has previously been considered to reduce the energy required to maintain a constant body temperature (Lovegrove et al., 1991a). When the body temperature (T_b) of non-torpid mammals is lower than that of the ambient, i.e. at high, potentially hyperthermic T_as, a low C_{min} is advantageous since it minimises heat flow into the animal. Similarly, at low ambient temperatures, i.e. at potentially hypothermic T_as, a low C_{min} minimises heat loss from the animal due to the temperature differential between the body and the ambient temperature. In numerous studies, desert rodent species have been shown to have lower thermal conductances than their non-desert counterparts, (Dawson, 1955; McNab & Morrison, 1963; Goyal et al., 1982; Haim, 1984; Gorecki et al., 1990; Lovegrove et al., 1991a).

Circadian energetic parameters: A less obvious energy–saving adaptation is that associated with endogenous circadian rhythms of metabolism and body temperature.

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The circadian rhythms typically consist of elevated T_bs and metabolism during an endotherm's active phase (α), and depressed values during its resting phase (ρ) (Aschoff & Pohl, 1970). The circadian rhythm of T_b is the outcome of the relationship between heat production and heat dissipation (Aschoff, 1982). Circadian increments in body temperature are generated by endogenous increments of metabolic rate which are thought to be further influenced by circadian rhythms of thermal conductance of the animal (Ashoff and Pohl, 1970; Aschoff, 1982). The maintenance of a sustained, elevated body temperature during the active phase is energetically costly. It also results in a high circadian amplitude of body temperature (R_t). However, a higher than expected R_t need not necessarily represent an additional cost to the animal. It may simply be a result of differences in heat-dissipating abilities or a lower than expected BMR (Lovegrove & Heldmaier, 1994), in which case it would represent an energy-saving advantage to the animal. A low, inflexible, conductance does not facilitate increased heat loss at the onset of the activity phase and consequently body temperatures rise higher than expected in response to circadian endogenous heat production rhythms. An appropriate comparison and quantification of the costs of circadian energetic rhythms can therefore only be made with measurements of the amplitude of metabolic rhythms taken simultaneously with measurements of circadian T_b rhythms (Lovegrove & Heldmaier, 1994).

The maximum body temperature during the active phase ($\alpha T_{b,max}$) appears to be independent of body size (Aschoff, 1982) and may represent a fairly inflexible optimal body temperature required for optimal metabolic and locomotory activity during the active phase. Reductions in minimum body temperature during the rest phase ($\rho T_{b,min}$) could represent energy conservation responses (Lovegrove & Heldmaier, 1994).

Body temperature (T_b): One model which attempts to account for the regulation of a constant deep body temperature in endotherms is Hammel's (1968) Hypothalamic Setpoint Hypothesis. This model proposes that an animal's body temperature is regulated with respect to a 'reference' setpoint body temperature (T_{set}). In order for enzymes to function optimally and thereby permit animals to be potentially active irrespective of the ambient temperature, the internal temperature of the animal should not fluctuate by more than a few degrees around this setpoint temperature (Lovegrove

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et al., 1991b). Although the setpoint T_b remains a conceptual physiological trait which cannot be measured directly, the minimum daily body temperature ($T_b$min) at the lower critical limit of thermoneutrality is the closest approximation of T_{set} (Lovegrove *et al.*, 1991b).

Processes resulting in the maintenance of thermal balance by the animal can be described and related by the simplified Newtonian equation $MR = C(T_b - T_a)$, where C is a measure of the thermal conductance of the animal, MR is the metabolic rate of the animal and T_a the ambient temperature (Scholander *et al.*, 1950). For an animal to maintain a constant T_b over an appreciable range of T_as below the lower critical limit of thermoneutrality, it must increase its metabolic heat production (Lovegrove *et al.* 1991b). A low mean or minimum body temperature (T_{set}) at thermoneutrality and at temperatures below thermoneutrality, may thus reduce the metabolic demands of maintaining a constant body temperature and may therefore represent an energy-conservative trait.

Under conditions of cold stress, T_{set} may be masked by responses such as increased thermal gradients between the core and the skin of mammals. Such masking may or may not conceal proximate thermoregulatory responses to cold stress, such as a reduction in either the mean or the setpoint T_b (reflected in a reduction in $T_b$min). The capacity for proximate adjustments to T_{set} during cold stress may be advantageous at low ambient temperatures since less heat production would be required to maintain body temperature. Conversely, however, a decrease in the ambient temperature may result in an increase in the setpoint T_b. An increase in T_{set} would require greater heat production to balance the additional heat loss to the environment generated by an increased $T_b - T_a$ gradient.

Two alternative models
I used the traits of basal metabolic rate, minimum thermal conductance, minimum body temperature, mean body temperature, daily energy expenditure and circadian amplitudes of body temperature and oxygen consumption, to test two alternative models concerning the adaptedness of mammals to energy stress in southern Africa. In addition, the proximate physiological responses of changes in body temperature (ΔT_b) and daily energy expenditure (Δ DEE) to cold stress, were also used to measure energy-

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saving capabilities:

Model 1: Model 1 hypothesises that the high temporal frequency of stresses in arid environments leads to strong selection for conservative physiological traits. These stresses arise from the high energetic costs of maintaining physiological homeostasis in arid environments (Parson, 1991) and the seasonal, spatial and temporal unpredictability of resource availability. Unpredictable resource availability arises as a direct result of the erratic fluctuations in interannual rainfall.

Model 1 therefore predicts that a gradient of conservatism of physiological traits will be detectable along an aridity gradient. There are two potential measures of the stresses associated with aridity; mean annual rainfall, and the co-efficient of variation of mean annual rainfall. Model 1 does not attempt to differentiate between these two measures. The model simply predicts a linear increase in the conservatism of traits with decreasing mean annual rainfall and increasing rainfall variability (Fig. 6). At some hypothetical point at the mesic end of the scale, the physiological trait should attain a value representing a biophysical/allometric limit or maximum, determined by the animal's body mass (Hayssen & Lacey, 1985; Bozinovic & Rosenmann, 1989; Bozinovic, 1992). Thereafter, it should show no further increase and should remain constant despite decreasing aridity (Fig. 6). This physiological limit may be expected to be reached in regions such as Mt Waialeale in Hawaii which experiences a mean annual rainfall of 11 680mm, the highest in the world. However, the maximum mean annual rainfall of the monsoon regions in southern Africa is less than 800mm (Fig. 8) and therefore it is presumed that traits do not attain this maximum at the upper limits of the eastern rainfall patterns. Therefore, in this study, I do not expect an assymptote in the physiological traits to be reached.

Model 2: Model 2 hypothesises that, in the southern African context, unpredictable periods of low habitat productivity generated by ENSO-related droughts mimic the aridity gradient effects predicted by Model 1.

Hence, Model 2 predicts that, although the stresses associated with unpredictable rainfall occur less frequently in non-desert ENSO zones, they are nevertheless sufficient to mimic the selection pressures of rainfall unpredictability in arid zones. Consequently, Model 2 predicts an increase in conservatism of physiological traits associated with a gradient of negative rainfall anomaly correlated with the ENSO

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(Fig. 6). The model predicts that physiological traits should once more become conservative at the eastern limits of the rainfall gradient, because it is these regions which are afflicted by ENSO (Fig. 3).

Study species

The four-striped field mouse, *Rhabdomys pumilio*, was chosen as the study species to test the models because it is widespread throughout southern Africa (Skinner & Smithers, 1990). It is an opportunistic omnivore which occurs in a wide variety of habitats, but is typically a grassland species (Skinner & Smithers, 1990). The species is thought to be crepuscular, with peaks of activity in the early morning and late afternoon (Skinner & Smithers, 1990).

Materials and Methods

Study areas

Study animals were captured from Aus (26°38'S;15°06'E), Goageb (26°45'S;17°14'E), Keetmanshoop (26°35'S;18°08'E), Rietfontein (26°45'S;20°02'E), Vanzylsrus (26°43'S;22°03'E) and Potchefstroom (26°44'S;27°04'E) in January and February 1996 (Fig. 7). These sites were chosen because they occur as close as possible to the 27° latitude thus limiting possible latitudinal effects. The areas represent an aridity gradient across southern Africa with the co-efficient of variation of mean annual rainfall providing an index of rainfall unpredictability (Fig. 2). Aus and Goageb are typically xeric with low and erratic annual rainfall (Fig. 8). Potchefstroom is mesic in that it is characterised by a more predictable rainfall pattern with a mean annual rainfall in excess of 500 mm (Fig. 8). In the southern African context, mesic regions are characterised as those regions which have a mean annual rainfall of above 500 mm (Lovegrove, 1993). Vanzylsrus, although it has low annual rainfall, has predictable rainfall patterns characteristic of a mesic area (Fig. 8). Keetmanshoop and Rietfontein are intermediate with respect to the xeric-mesic gradient. The rainfall patterns in these two sites are less erratic than those of xeric regions, but are more unpredictable than the rainfall patterns of mesic regions (Fig. 8). Potchefstroom and Vanzylsrus occur within the region of southern Africa which experiences negative rainfall anomalies during El Niño Southern Oscillation events

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(Fig. 3) (Stone *et al.*, 1991). In general, Potchefstroom and Vanzylsrus received approximately 77% of their mean annual rainfall during ENSO events (Fig. 4).

Another source of climatic variation between the sites is the diel and seasonal amplitude of ambient temperature (Table 1).

Study animals

R. pumilio were trapped in January and February 1996 from the above sites using Sherman box traps baited with peanut butter and oats. They were transported by road to Pietermaritzburg. They were housed in a constant environment room in conventional rodent cages (40cm X 25cm) at an ambient temperature of 25°C and a photoperiod of 12L:12D. The mice were fed a diet of dry rodent pellets, apple and carrot, and were weighed weekly.

Measurement of Tb

Temperature-sensitive telemeters (Mini-mitter Model XM), calibrated with a standard mercury thermometer (0.05°C) in a water bath between 5 and 45°C, were implanted into the intra-peritoneal cavity under inhalation anaesthesia (Isoflourane; induction, 2% in O_2; maintenance, 1.2% in O_2; flow rate, *ca* 0.5 l.min^{-1}). Signals transmitted by mini-mitters were detected using antennae attached to perspex sleeves surrounding the respirometers in which measurements were made. Signals were converted to TLL waves using a monostable multi-vibrator and then converted to voltages using a frequency-to-voltage converter. The ambient temperatures in the cabinet and respirometers were measured using thermistor probes, calibrated in a similar manner.

Metabolic measurements

All metabolic measurements were made in 2.5 dm^3, dome-shaped respirometers (18cm long, 12cm wide, 12cm high) constructed from clear perspex. Respirometers were placed in a 1 m^3 sound-proof constant environment cabinet with a light:dark cycle of 12L:12D. Measurements of VO_2 were made using an open flow-through system. Atmospheric air, acting as the control gas, was pumped from outside the building, into the cabinet at approximately 5 l.min^{-1}, and partially dried using silica gel (relative humidity < 50%). This air was drawn through the respirometers at flow rates of

approximately $1.2\,\ell.\text{min}^{-1}$, chosen to maintain less than 1% oxygen depletion between the incurrent and the excurrent air. The flow rate was measured with a Brooks Thermal Mass Flow Meter (Model 5810), factory calibrated to STP at sea level. The use of solenoid valves and a pump for each respirometer allowed five respirometers, as well as a control channel, to be used simultaneously. The excurrent air from each respirometer was passed, via CO_2-proof tubing, through a water condenser and a CO_2 scrubber to remove water vapour and CO_2 gas, respectively. After passing through the pumps, relay valves, filters and the mass flow meter, the excurrent air was subsampled with an Applied Electrochemistry Oxygen Analyser (Model S-3A/1, Ametek) and an Oxygen Sensor (Ametek N-22M) to determine the fractional concentration of oxygen in the dry air. Analogue signals from the thermistor probes, mini-mitters, mass flow meter and oxygen analyser were digitised using an A/D converter and recorded on a multi-channel, custom-written WINDOWS-based recording program, with a sample interval for each respirometer of six minutes. Metabolic rates were calculated using the equation $VO_2 = V_E(F_{IO2} - F_{EO2})/(1 - F_{IO2})$ where VO_2 = metabolic rate ($m\ell\,O_2.h^{-1}$), V_E = flow rate ($m\ell.\text{min}^{-1}$), F_{IO2} = incurrent fractional O₂ concentration and F_{EO2} excurrent fractional O_2 concentration (Withers, 1977).

Experimental protocol
Determination of the lower critical limit of thermoneutrality (T_{lc})
To determine the lower critical limit of thermoneutrality, the rodents were placed in respirometers at an ambient temperature of 25°C at 17h30 on the day prior to measurements. Apple was provided for the duration of the dark period but was removed at 5h30 the following day before measurements commenced. Measurements commenced at 6h00 and ended at 12h00. This time period was chosen for measurements as preliminary trial runs showed this to be the period during which the animals were least active. Oxygen consumption was measured for two hours at each ambient temperature (T_a); 5°C, 15°C, 25°C, 30°C, 32°C, 34°C and 36°C. Resting metabolic rate (RMR) was calculated as the mean of the three lowest consecutive data points during the last 30 min at each temperature. This ensured that at the time of calculation of RMR, animals had responded to the change in T_a and metabolic rate had stabilized for a period of at least 18 minutes. Linear regressions of RMR as a function

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of T_a at $T_a < 32°C$ were calculated for each animal using the method of least squares fit (Zar, 1984). Individual T_{lc} values were calculated as the intercept of this line with the BMR calculated from the lowest RMR values at T_as > 32°C. The mean T_{lc} for each site was calculated using the respective individual T_{lc} values.

Minimum wet thermal conductance (C_{min}) was taken as the slope of the regression line of RMR as a function of T_a at $T_a < 32°C$ (Scholander et al., 1950)

Measurements of circadian rhythms of body temperature and metabolism
Body temperature and oxygen consumption were measured over a period of 24 hours, from 12h00 to 12h00 the following day at T_a = 30 °C and T_a = 20 °C. These two temperatures thus measured circadian rhythms both within the thermoneutral zone, thereby excluding thermoregulatory effects (T_a = 30 °C), and at ambient temperatures below the lower critical limit of thermoneutrality (T_a = 20 °C), thus including thermoregulatory effects . Animals were placed in respirometers 30 minutes prior to the commencement of observations and were provisioned with apple and dry rodent pellets throughout the period of observation.

From these circadian measurements, average body temperature (T_b), total oxygen consumption (VO_2), and minimum and maximum values of T_b and VO_2 were obtained. To describe the circadian energetic rhythms of *Rhabdomys pumilio*, mean T_b and total VO_2 values were calculated for the total 24h observation period, as well as for the periods 12h00 to 18h00 (pm), 18h00 to 6h00 (night), 6h00 to 12h00 (am) and 12h00 to 18h00 combined with 6h00 to 12h00 (day). These time periods were selected because of the lack of any *a priori* knowledge of whether the activity pattern of this species is nocturnal, diurnal or crepuscular. It has been suggested that the species is crepuscular (Skinner & Smithers, 1990), and hence the parameters were analysed during these specific time periods to best describe the behaviour of crepuscular endogenous rhythms.

Maximum and minimum values of T_b and VO_2 were objectively calculated as the mean of the three highest and three lowest consecutive points during the 24h cycle. The use of three consecutive points to calculate these values eliminated the possibility of single, artifactual points providing biased estimates of maxima and minima.

Circadian amplitudes of T_b (R_t) and VO_2 (R_{VO_2}) were calculated by subtracting the

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calculated minimum values of T_b or VO_2 from the calculated maximum values of T_b or VO_2.

The changes in the animals' thermoregulatory responses at different T_as were observed by calculating differences in average T_b and total VO_2 between the $T_a = 30°C$ and $T_a = 20°C$ trials.

Estimates of energy expenditure were calculated from VO_2 data assuming a conversion factor of 20.08 kJ/ ℓO_2; the mean value for heat produced per litre of O_2 consumed for carbohydrate, protein and fat metabolism (Schmidt-Nielsen, 1983). The largest error that can result from the use of this value is 6%, which would occur if the animals were metabolizing either pure protein or pure carbohydrate. Usually the error is insignificant if the metabolic fuel is a mixture of fat, carbohydrate and protein (Schmidt-Nielsen, 1983), which is likely given the mixed diet fed to the mice.

Data analysis

To describe the metabolic and body temperature circadian rhythms of *R. pumilio*, data for all sites were pooled. These data were used to determine differences in metabolic activity during different circadian time periods and at different T_as. Wilcoxan signed rank tests for paired, non-parametric data were used in these comparisons of body temperature and oxygen consumption.

All data were tested for homogeneity of variance using a Bartlett's test (Zar, 1984). Where data sets were found to have heterogenous variances, a non-parametric Kruskal-Wallis test for intergroup differences (Zar, 1984) was used to test for trait differences between sites. A *posteriori* Scheffé Range test was used to determine specific site differences.

All statistical procedures were performed using either STATGRAPHICS (STSC, U.S.A) or QUATTRO PRO V 6.0 (Novell, U.S.A) software packages.

Model 1 was tested by fitting a simple linear regression (Zar, 1984) to the trait (dependent variable) plotted as a function of the co-efficient of variation of mean annual rainfall (independent variable). Model 2 was tested by fitting a second order polynomial regression to the same data.

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Results

Thermoregulatory data

The body masses of the mice did not differ significantly between sites (Kruskal-Wallis test, H = 7.46, p > 0.05). The mean body mass of all animals at the commencement of VO_2 measurement was 55.09 ± 5.36g (n = 30) (Table 3). This mean mass was higher than that of 45.7g reported for *R. pumilio* at capture from the southwest Kalahari, Botswana (Skinner & Smithers, 1990). However *R. pumilio* have been shown to vary in size from different geographical regions in southern Africa (Skinner & Smithers, 1990).

The mass-specific oxygen consumption of all mice increased linearly with a decrease in ambient temperature (T_a) between 5 and 30°C (Fig. 9). Minimum wet thermal conductances (C_{min}), calculated for each rodent as the slope of the change in VO_2 as a function of T_a, did not differ significantly between sites (Kruskal-Wallis test, H = 9.52, p > 0.05; Table 3). The mean thermal conductance of all animals was 0.110 ± 0.021 ml O_2/g/h/°C (n = 30).

The basal metabolic rate, defined here as the minimum oxygen consumption at thermoneutrality, did not differ significantly between sites (Kruskal-Wallis test, H = 8.43, p > 0.05). However, the results suggest a clinal increase towards the east (Table 3), which was inversely related to the aridity gradient. The mean BMR for all rodents was 0.819 ± 0.084 ml O_2/g/h (n = 30).

The average lower critical limit of thermoneutrality (T_{lc}) for all study animals was 30.59 ± 2.17°C. There were no significant differences in the T_{lc}s of the animals from the different study sites (Kruskal-Wallis test, H = 8.95, p > 0.05; Table 3).

Circadian parameters

Circadian rhythms of metabolism and body temperature.

In general, the circadian changes in body temperature (T_b) and oxygen consumption (VO_2) of *R. pumilio,* both at thermoneutrality (Figs 10 & 12), and at T_a = 20°C (Figs 11 & 13), showed a two-peak, bimodal pattern confirming their crepuscular habit (Skinner & Smithers, 1991). This pattern was characterised by an evening and a morning peak in T_b and VO_2. The increase in T_b and VO_2 leading to the evening peak occurred prior

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to the onset of dark (18h00). After reaching a peak, either prior to or after the onset of dark, T_b and VO_2 decreased steadily. The onset of the increase in T_b and VO_2 leading to the morning peak occurred prior to the onset of light (6h00). After reaching a peak, either prior to or after the onset of light, T_b and VO_2 decreased steadily. The evening peak of T_b and VO_2 tended to be higher than the morning peak.

Following the evening peak, and prior to the morning peak (during the scotophase), a period of reduced body temperatures and oxygen consumption occurred. Reduced T_bs and VO_2 also occurred between the morning and evening peaks but were not as low as those during the scotophase.

The occurrence of periods of high T_b and VO_2 and periods of low T_b and VO_2 are confirmed by the time of occurrence of the maximum and minimum body temperatures and oxygen consumption of the rodents (Figs 14 & 15). Body temperatures and oxygen consumption of most rodents reached a maximum either between 12h00 and 20h00 or between 3h00 and 12h00. Minimum T_bs and VO_2 were reached mostly between 20h00 and 4h00, but also between 6h00 and 12h00 in most rodents.

The Aus mice were the only exceptions to the two-peak pattern of circadian changes in T_b and VO_2. At thermoneutrality the peaks in body temperature and oxygen consumption were less obvious (Fig. 10). However at $T_a = 20°C$, their daily changes of T_b did show a bimodal pattern (Fig. 11).

At $T_a = 20°C$ the pattern of circadian changes in oxygen consumption of rodents from all sites was not clearly defined (Fig. 13). Presumably, this arises because the pattern becomes masked by increases in VO_2 associated with thermoregulatory responses at this ambient temperature. However a weak bimodal pattern was still evident in the circadian rhythms of oxygen consumption of the rodents at thermoneutrality.

The above descriptions of the circadian rhythms of body temperature and oxygen consumption of R. pumilio can be confirmed and further described and quantified by comparing mean body temperatures (Tables 3 & 4) and energy expenditure (Tables 5 & 6) of the rodents during different time periods.

At both thermoneutrality ($T_a = 30°C$) and at $T_a = 20°C$, mean T_b during the day (6h00 - 18h00) was significantly higher than at night (18h00 - 6h00) (Table 7). Furthermore, the body temperature of R. pumilio showed a proximate physiological

response to ambient temperature. At $T_a = 20°C$, the nightly decrease in T_b (Table 7) was significantly higher than at thermoneutrality (Wilcoxan signed rank test, $z = 4.77$, $p < 0.01$).

Interestingly, there was no significant difference in energy expenditure between the day and the night periods at either ambient temperature (Table 7). Since the body temperatures of the animals were significantly higher during the day, and body temperature is affected by energy expenditure, this was not expected.

Energy expenditure and mean body temperatures were significantly higher during the evening (pm) period than during the morning (am) period (Table 7). This indicates that the evening peaks of T_b and VO_2 were higher and of longer duration than the morning peaks.

The body temperature and energy expenditure of R. pumilio showed proximate responses to cold stress. These responses are reflected in changes in the mean T_bs (Table 8), energy expenditures (Table 9), circadian amplitudes of T_b and VO_2 (Table 10), and minimum body temperatures (Table 11), with ambient temperature.

The mean and minimum body temperatures of R. pumilio were significantly lower at $T_a = 20°C$ than at thermoneutrality (Table 12), whereas the daily energy expenditure of the rodents was significantly higher (Table 12).

Circadian amplitudes of body temperature (R_t) and oxygen consumption (R_{VO_2}) were both significantly higher at the lower ambient temperature than at thermoneutrality (Table 12)

The minimum body temperatures (T_{bmin}) at $T_a = 20°C$ were significantly lower than at thermoneutrality (Table 12).

Geographic variation in phenotypic traits

At thermoneutrality, the mean body temperatures and daily energy expenditure of the animals showed significant variation between sites (Table 13). The mean T_b of animals from Rietfontein was significantly higher than those of animals from Goageb whereas the mean T_bs of animals from Aus, Keetmanshoop, Vanzylsrus and Potchefstroom were similar (Scheffe range test). Animals from Vanzylsrus expended significantly less energy over the 24-hour period than did the animals from Aus, Keetmanshoop and Rietfontein. The animals from Potchefstroom showed no difference to the animals from

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Goageb in terms of their daily energy expenditure (Scheffe range test).

The daily energy expenditure of the animals at an ambient temperature of 20°C also showed significant geographic variation (Table 13). The daily energy consumption of animals from Goageb and Potchefstroom was significantly lower than that of animals from Rietfontein (Sheffe range test). At this ambient temperature, as at thermoneutrality, the DEE of animals from Goageb was not different to that of animals from Potchefstroom (Sheffe range test). At T_a = 20°C, the animals from Vanzylsrus, Aus and Keetmanshoop were also homogenous in terms of their DEE (Sheffe range test).

The proximate responses of body temperature (ΔT_b) and daily energy expenditure (ΔDEE) to cold stress also showed significant geographic variation (Table 13). When comparing the body temperatures of the animals at T_a = 30°C and at T_a = 20°C, the animals from Potchefstroom showed a significantly greater difference in T_b between these two ambient temperatures than animals from Goageb. When comparing the DEE of the animals at T_a = 30°C and at T_a = 20°C, animals from Rietfontein and Vanzylsrus showed a significantly higher difference in their energy expenditure between these two ambient temperatures than animals from Goageb.

The models

The models were tested using both mean annual rainfall and the co-efficient of variation of mean annual rainfall as indications of the aridity gradient. In all cases the co-efficient of variation of mean annual rainfall accounted for more of the variation in phenotypic traits and proximate responses than did the mean annual rainfall.

Basal metabolic rate (Fig. 16), mean body temperature at T_a = 30°C (Fig. 17), and the reduction in body temperature under conditions of cold stress (Fig. 20), all showed significant linear trends with the co-efficient of variation of mean annual rainfall (Table 14). They all showed a decrease with increasing rainfall variability, as predicted by Model 1. However for all three of these traits and proximate responses, a second order regression fitted as a function of the co-efficient of variation of mean annual rainfall, gave a higher co-efficient of determination than that for a first order regression (Table 14) i.e. Model 2 accounted for more of the variation in the phenotypic traits and proximate responses of the animals than did Model 1. Basal metabolic rate (Fig. 16),

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mean T_b at $T_a = 30°C$ (Fig. 17), DEE at $T_a = 30°C$ (Fig. 18) and at $T_a = 20°C$ (Fig. 19), $\triangle T_b$ (Fig. 20) and $\triangle DEE$ (Fig. 21), all showed a significant parabolic relationship with the co-efficient of variation of mean annual rainfall (Table 14). In these cases the variation in the physiological traits and proximate responses of the animals were significantly described by Model 2. The parabolic relationship is particularly evident in the variation in mean body temperature at $T_a = 30°C$ (Fig. 17), daily energy expenditure at $T_a = 30°C$ (Fig. 18) and at $T_a = 20°C$ (Fig. 19), and the change in DEE with ambient temperature (Fig. 21). In general these traits and proximate responses are conservative (low) in areas with high annual rainfall variability (arid regions) and show an initial increase as rainfall variability decreases (as predicted by Model 1 and 2). However after this initial increase, the traits and proximate responses show a decrease (i.e. an increase in conservatism) with decreasing annual rainfall variability. This increase in the conservatism of traits and proximate responses was inversely related to annual rainfall variability and was not predicted by Model 1 but was predicted by Model 2 as an effect of infrequent rainfall unpredictability associated with ENSO.

Discussion

Basal metabolic rate

The BMR of 0.819 mlO_2/g/h of *R. pumilio* in this study, compared well with the BMR of 0.81 ± 0.09 mlO_2/g/h previously reported for this species (Haim & Fourie, 1980). It is however 59% lower than that predicted on the basis of body weight alone (Kleiber, 1961), and 38% lower than that predicted by Hayssen & Lacy's (1985) rodent curve for a 55g animal. This lower than expected BMR translates into energy savings for individuals, as it minimises energy costs yet permits animals to maintain homeothermy nevertheless.

A low BMR has previously been considered to represent an adaptation to an arid environment (McNab and Morrison, 1963; McNab, 1966, Schmidt-Nielsen, 1972; McNab, 1979; Haim, 1984; Lovegrove, 1986; Gorecki, Meczera, Pis, Grasimov & Walkowa, 1990; Lovegrove, Heldmaier & Knight, 1991;Rubal, Choshniak & Haim, 1992; Haim & Izhaki, 1993). Since most regions in southern Africa can be categorised as arid, i.e. having a mean annual rainfall <500 mm (Fig. 1) (Lovegrove, 1993), the low BMR of

this southern African rodent species was not unexpected. Furthermore, although there was no significant difference in the BMR of the animals from the different sites, the clinal increase in BMR, inversely related to the aridity gradient, lends further support to the hypothesis that aridity provides a selection pressure for low rates of metabolism. The particular feature of arid environments which provides this selection pressure, will be discussed later.

Thermal conductance

The minimum wet thermal conductance of 0.110 $mlO_2/g/h/°C$ of *R. pumilio* in this study, was lower than that of 0.166 ± 0.017 ml $O_2/g/h/°C$ previously reported for this species (Haim & Fourie, 1980). This may be because the rodents used in the Haim & Fourie study (1980) were smaller than those used in this study. Since it is known that thermal conductance is inversely related to body weight (McNab, 1970), the discrepancy is not unexpected. However, the C_{min} of *R. pumilio* in this study was 81% of that predicted by the equation for rodent thermal conductance (McNab & Morrison, 1963) and 73% of that predicted by Aschoff's (1981) equation for mammalian thermal conductance. It must be noted that both of these equations have limitations. In many of the data sources used to formulate these equations, no distinction was made between active and resting phase thermal conductances (Aschoff, 1981). Since it has been shown that minimal conductance is subject to circadian variation (Aschoff & Pohl, 1970), this may account for some of the deviation of the C_{min} of *R. pumilio* in this study from predicted values. Nevertheless, a C_{min} 20% below the predicted value need not be explained by circadian phase alone. The low thermal conductance of this species may be explained, in addition, by its low rate of metabolism. Due to the low metabolic rate, the rodents can maintain a normal mammalian body temperature only through a lower thermal conductance. Furthermore, by minimising heat flow into and out of the animal, this low thermal conductance reduces the energy required to maintain a constant body temperature at ambient temperatures above and below the body temperature (Lovegrove *et al.*, 1991a). Combined with its low basal metabolic rate, the low thermal conductance will also reduce the need for evaporative cooling at high ambient temperatures. This will serve to minimize evaporative water loss in this species, an important attribute in arid environments where water is a valuable resource. Low

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thermal conductances have previously been reported for numerous desert rodent species (Dawson, 1955; Mc Nab & Morrison, 1963; Goyal et al., 1981; Haim, 1984; Gorecki et al., 1990; Lovegrove et al., 1991a).

Minimum wet thermal conductance did not show a significant trend with the aridity gradient (Table 14). Thermal conductance may, however, be a function of additional environmental variables not examined in this study, such as ambient temperature (minimum and maximum) and altitude. Concerning ambient temperature for example, Lovegrove et al., 1991a, have argued that the maximum seasonal and diel range of ambient temperature may determine the C_{min} of small mammals. If this is the case, then C_{min} will also depend upon the degree to which the animals are able to avoid exposure to high and low ambient temperatures by behavioural means.

R. pumilio is characterised by black pigmentation of its skin. It has been suggested that animals with black skin are able to convert solar radiation into heat, thereby reducing metabolic requirements to maintain a constant body temperature (Dmi'el et al., 1980). Since the study animals had no access to solar radiation during the thermoregulation measurements the value of C_{min} reported here may bear little relevance to the ease with which heat enters or leaves the bodies of these rodents under natural conditions.

Circadian rhythms of body temperature and oxygen consumption
In general, the circadian changes of body temperature and oxygen consumption of the four-striped field mouse in this study showed a pattern confirming the crepuscular nature of this species. The pattern was characterised by a peak in T_b and VO_2 in the evening, and smaller peaks in the early morning. Between these two peaks, body temperatures and oxygen consumption were reduced. Since increases in oxygen consumption and body temperature are usually indicative of periods of activity (Aschoff, 1970), these patterns suggest that R. pumilio is generally active in the evenings and early mornings. These periods of activity allow individuals to avoid the hotter hours of the day, thereby reducing both thermoregulatory energy usage and evaporative water loss.

The reduced morning peak in T_b compared with the evening peak may not be a true indication of what occurs under natural conditions. It may simply be the result of

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the absence of solar radiation in the laboratory. Because of its black skin, this species may, under natural conditions, convert early morning solar energy into heat energy, thus increasing body temperature at no thermoregulatory cost.

Nevertheless, the circadian rhythms of body temperature are usually the outcome of the relationship between heat production and heat dissipation (Aschoff, 1982). The reduced body temperatures during the scotophase may either be a result of increased thermal conductance or decreased metabolic rate. An increase in thermal conductance during the rest phase, whilst maintaining a constant rate of heat production, will result in an increase in the rate of heat dissipation with a concomitant decrease in body temperature. Alternatively, conductance may remain unchanged whilst metabolic rate is reduced during the rest phase, resulting in a decrease in body temperature. In the case of *R. pumilio*, however, it seems that the changes in body temperature could best be attributed to changes in metabolic rate. Comparing the metabolic rate (Figs 12 & 13) and body temperature (Figs 10 & 11) circadian data, an increase in body temperature was preceded by an increase in oxygen consumption. This result may suggest that *R. pumilio* behaves like the pouched mouse (*Saccostomus campestris*), in which the VO_2 rhythm, rather than the conductance rhythm, was found to underly the T_b rhythm (Haim, Racey, Speakman, Ellison & Skinner, 1991).

An analysis of the circadian amplitudes of body temperature and oxygen consumption of *R. pumilio* showed that these traits increase the energy-saving ability of this species. At thermoneutrality, the circadian amplitudes of body temperature and oxygen consumption were respectively 17% and 21% higher than predicted by Aschoff (1982) for a 55g animal. These higher circadian amplitudes of T_b and VO_2 were generated by low rest-phase metabolic rates, resulting in lower daily rates of energy expenditure. Although there was no significant difference between the day and the night energy expenditure (Table 7), oxygen consumption was clearly reduced during the scotophase (Fig. 12). The depressed metabolic rate during the rest phase of the animals was obscured in statistical analysis because the period chosen to indicate the rest phase, i.e. the "night" period, included the increase in oxygen consumption preceding the morning peak in metabolic rate.

The proximate responses of *R. pumilio* to cold stress also indicated evidence of energy conservatism. Although energy expenditure was higher at the colder

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temperatures due the enhanced thermoregulatory cost, the animals' mean and minimum body temperatures were significantly lower than they were at thermoneutrality (Table 12). The ability to maintain a lower body temperature under conditions of cold stress clearly confers energetic benefits on this species, as less energy is required to maintain the body temperature. Furthermore, the circadian amplitudes of body temperature and oxygen consumption were significantly higher under conditions of cold stress than at thermoneutrality (Table 12). It can therefore be deduced that the reduction in body temperature at the lower ambient temperature, occurred mostly during the rest phase when the animals were inactive. This rest-phase reduction in body temperature at low ambient temperatures results in the conservation of energy without reducing the animals' ability to carry out normal activity during the active phase.

Energetic adaptations

Allometric correlates with body mass have been established for physiological variables such as basal and resting metabolic rates (Kleiber, 1961; Aschoff, 1982; Hayssen & Lacey, 1985), thermal conductance (McNab & Morrison, 1963; Aschoff, 1981;) and circadian amplitudes of body temperature and oxygen consumption (Aschoff, 1982). Deviations from expected values might be explained by physiological adaptations to different environmental conditions. *R. pumilio* occurs widely across southern Africa and, since most regions in southern Africa are arid regions i.e. have a mean annual rainfall of less than 500 mm (Fig. 1) (Lovegrove, 1993), most *Rhabdomys* populations are subject to some degree of aridity stress. Aridity stress, as Parsons (1991) explains, results in physiological energy stress. The deviations of the values of BMR, thermal conductance and circadian amplitudes of body temperature and oxygen consumption of *R. pumilio* from expected values, may thus be explained in terms of their adaptive benefits to this energy stress. *R. pumilio* has both a BMR and a thermal conductance lower than those predicted by allometric equations. These conservative traits confer energetic benefits on the animals by reducing thermoregulatory costs as well as minimizing evaporative water loss. The higher-than-expected circadian amplitudes of body temperature and oxygen consumption also reduce daily energy requirements and minimize energy stress. The ability to reduce their body temperatures, and increase their circadian amplitudes of body temperature and oxygen consumption, under

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conditions of cold stress, also increase the adaptedness of *R. pumilio* to arid environments. So too should the black skin and the crepuscular activity patterns of this species. Furthermore, *R. pumilio* has been reported to possess the capacity to store and mobilize fat and capitalize on preformed water available in food (Willan & Meester, 1987). These abilities can also be seen as adaptations to an arid environment.

Another aspect that was apparent in this study was the large amount of physiological variation within population subsamples. It is not certain whether the variation is a) larger than that measured in other rodents; b) true phenotypic variation or, c) a consequence of environmental and parental developmental effects (Gould & Johnson, 1972). As Parsons (1995) explains "... genetic variation may be the ultimate limiting factor determining whether free-living populations can adapt to changing environments". In other words, the high genetic variation of this species preserves its evolutionary potential, enabling it to adapt to different environments.

Geographic variation in physiological traits
The hypothesis that physiological traits of rodents from regions subject to severe aridity stresses e.g. Goageb and Aus, will be more conservative than those of rodents from regions subject to less severe aridity stresses e.g. Vanzylsrus and Potchefstroom, could not be confirmed in this study. Instead, it was shown that, at thermoneutrality, and under conditions of cold stress, the daily energy consumption of animals from the mesic region of Potchefstroom did not differ from that of animals from the desert region of Goageb. Moreover, the daily energy expenditure at thermoneutral temperatures of animals from Vanzylsrus was lower than those of animals from Aus, Keetmanshoop and Rietfontein, despite these three regions being subject to more severe aridity stresses than Vanzylsrus. However, under conditions of cold stress, rodents from Rietfontein had higher daily energy requirements than rodents from Goageb and Potchefstroom. This latter finding could indicate that aridity effects have resulted in selection for conservative rates of metabolism in animals from Goageb, and that this selective pressure weakens eastwards at Rietfontein.

What ecological stress then, has selected for the conservative energetic traits, both at thermoneutrality and under conditions of cold stress, in animals from Potchefstroom, an essentially mesic environment? We may ask this same question to

account for the low thermoneutral daily energy expenditure of animals from Vanzylsrus. It seems that, in terms of the selection for energy conservative traits, the effects of the southern African aridity gradient can be seen from Goageb to Rietfontein, whereafter another ecological feature, not related to aridity, is implicated in the selection of conservative rates of energy expenditure in the regions of Vanzylsrus and Potchefstroom. This study argues that, since these two study sites lie in the region affected by ENSO events (Figs 3 & 4), the low rates of energy expenditure seen in the rodents from these areas may have been selected for by an aridity-mimicry effect of the El Niño phenomenon, as predicted by Model 2.

Aridity effects may also explain the lower body temperatures at thermoneutrality of rodents from Goageb, compared with those for rodents from Rietfontein. Goageb is a more arid region than Rietfontein, and therefore the stresses associated with aridity are more severe in Goageb than in Rietfontein. A lower body temperature at thermoneutrality reduces daily energy requirements and may be seen as an adaptation to these stresses. Geographic variation in the T_b trait provides further evidence that a non-aridity related factor has affected the selection of physiological traits of the rodents from Vanzylsrus and Potchefstroom. The body temperatures at thermoneutrality of the rodents from these two regions did not differ from those of rodents from more arid regions, despite the reduced aridity stresses in Vanzylsrus and Potchefstroom. Again this indicates that ENSO-related energy stresses may have led to strong selection for reduced body temperatures in these regions.

The geographical variation in body temperatures recorded at thermoneutrality was not evident under conditions of cold stress. This may be due to differences in the thermoregulatory response of the animals to these conditions. Nevertheless, all the animals showed lower body temperatures than those measured at thermoneutrality when subjected to conditions of cold stress. This conservative proximate response of body temperature did indeed show significant geographic variation. Animals from Potchefstroom, a mesic region, showed a higher reduction in their circadian body temperatures when subjected to cold conditions, than did animals from Goageb, a region subject to severe aridity stresses. Since a reduced body temperature at low ambient temperatures is thought to be a mechanism whereby energy requirements can be reduced, this less conservative response in animals from Goageb was not expected.

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However, under conditions of cold stress, the DEE of animals from Goageb was as low as that of animals from Potchefstroom. This may indicate that animals from Goageb employ other mechanisms of reducing thermoregulatory costs, such as a reduction in their thermal conductance. Furthermore, the additional energy ($\triangle$DEE) required for the necessary thermoregulatory responses at low ambient temperatures was lowest in the animals from Goageb. This indicates that the response of these animals to cold stress was obviously the least energy expensive. It could be argued that this response has been selected for by the severity of aridity stresses in this region as it is significantly more energy conservative than those thermoregulatory responses utilized by animals from the less arid regions of Rietfontein and Vanzylsrus.

The elevated thermoregulatory costs of animals from Vanzylsrus when subjected to cold stress was not expected. Due to the energy stresses experienced in the Vanzylsrus area during previous ENSO events, it is logical that a less energy expensive response to cold stress would have been selected for in the rodents from this area by these ENSO-related energy stresses. This seemingly expensive response of the animals from Vanzylsrus to cold stress may be an artefact of the very low daily energy expenditure of these rodents at thermoneutral ambient temperatures. Indeed, the daily energy expenditure of the animals from Vanzylsrus at low ambient temperatures was no different to that of the animals from the more arid region of Aus.

The models

It was shown in this study that the co-efficient of variation of mean annual rainfall accounted for more of the geographic variation in phenotypic traits and proximate responses than did mean annual rainfall. This indicates that the unpredictability of rainfall, rather than absolute rainfall, exerts stronger selection pressure for conservative energetic traits in arid habitats. However, the hypothesis that the conservatism of physiological traits can be predicted on the basis of an aridity gradient alone (Model 1), did not hold for the southern African aridity gradient. Only three of fourteen physiological traits and proximate responses chosen to indicate evidence of the energy-saving abilities of individuals, showed a significant linear increase inversely related to annual rainfall variability. In contrast, the geographical variation in six of the physiological traits and proximate responses could be explained by Model 2, which

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considers the combined potential selection effects of aridity and ENSO-related rainfall unpredictability.

It could be argued that the number of traits and proximate responses showing geographic variation conforming to Model 2 may nevertheless provide insufficient support for the Model. If the ENSO-related energy stresses do mimic those of aridity, why does Model 2 not account for the geographic variation in all of the physiological traits and proximate responses examined?

Firstly, for all the traits and proximate responses tested, Model 2 accounted for more of the geographic variation than did Model 1. This indicates that El Niño related resource unpredictability has had at least a partial selective effect on the genetic composition of *Rhabdomys* populations in the ENSO-affected zones.

Secondly, the geographic variation of those traits which did not show a pattern predicted by Model 2, were mostly those traits which, for the species as a whole, were more conservative than predicted by allometric equations. The thermal conductances of *Rhabdomys* in this study were lower, and the circadian amplitudes of body temperature and oxygen consumption, higher, than those predicted on the basis of body weight. This indicates that these traits are already conservative relative to the global pattern for rodents. That these traits showed little geographic variation may suggest that they may have attained a physiological limit necessary for homeothermy. With the exception of proximate responses, further reduction in the thermal conductance, or a further increase in the circadian amplitudes of body temperature and oxygen consumption, may not facilitate adequate homeothermy in this species.

Another possible explanation why some traits and proximate responses are not more conservative in arid and ENSO-affected zones than they are in other zones in southern Africa, may be that it is not necessarily advantageous for all physiological traits to be energetically conservative. It may not be "necessary" for this species to utilize all of the potential pathways of adaptation to energy stresses. As Bartholomew (1987) explains, for a given habitat and any given biological problem, there is more than one solution. The few traits that are energetically conservative may be sufficient to allow the animals to survive and reproduce during the unpredictable periods of low habitat productivity that they experience. Additional conservative traits may not be necessary to optimise fitness. Indeed, additional conservatism may be deleterious as a correlated

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response to this selection is likely to be diminished available metabolic energy, expressed as reduced fitness under non-stressful conditions (Parsons, 1991). This would have a number of implications to this species. Firstly, *Rhabdomys* is an opportunist with fast growth rates and large litter sizes (Skinner & Smithers, 1990). Such characteristics of "r-selected" life-history strategies (*sensu* MacArthur & Wilson, 1967) have been thought to require high rates of metabolism (McNab, 1980; although see Harvey and Pagel, 1991) and therefore would not be possible if energetic traits were conservative. Secondly, if irreversible genetic responses to a stress do occur, the resulting physiological constraints would prohibit populations from responding further and may thereby restrict range extensions into increasingly harsh environments (Parsons, 1991). Reduced available metabolic energy may also restrict the evolution of phenotypic plasticity (Via, 1987). Phenotypic plasticity, an environmentally produced change in the phenotypic expression of a genotype (Bradshaw, 1965), is considered to be an alternate outcome of selection in a variable environment (Via, 1987). It can evolve in a variable environment by providing a selective advantage to the individuals that produce an appropriate environmental response (Bradshaw, 1965). Plastic responses to rapid changes in environments, such as low resource availability, are more effective than genetic changes because they are reversible and because genetic polymorphism involves a time lag in response through gene frequency changes (Levins, 1968). However, plasticity can only develop in a variable environment when there is sufficient available metabolic energy (Via, 1987). Therefore, additional conservatism in this species may have restricted the evolution of phenotypic responses to the environment.   Theoretically, phenotypic plasticity is likely to have evolved, to a variable extent, in this species. All of the populations studied were characterised by a high degree of genetic variation in their "reaction norms" which is necessary for the evolution of phenotypic plasticity (Levins, 1968). However, since maintaining a plastic phenotype is likely to entail a metabolic cost, selection against genotypes with a high level of plasticity is likely to occur in low variability environments (Bradshaw, 1985). Consequently, it could be expected that the levels of phenotypic plasticity in the arid and ENSO-affected zones are higher than in other zones. This may explain why Model 2 did not account for the geographic variation in some of the physiological traits tested. Under non-stressful laboratory conditions, the "norm-reaction" of some of the traits, did

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not differ geographically. However, when subjected to energy stress, these traits, in animals from the arid and ENSO-afflicted zones, may, by a phenotypic response, become more conservative.

One of the traits that did display geographic variation as predicted by Model 2, was BMR, suggesting evidence of selection by aridity and ENSO imposed stresses. In this study, BMR showed a clinal decrease inversely related to the aridity gradient. This pattern was predicted by Model 1, and was similar to that shown by the geographic variation in BMR of the Israeli mole rat, *Spalax ehrenbergi* (Nevo & Shkolnik, 1974). Other studies on the geographic variation of rodents have shown that the BMRs of rodents from arid zones are significantly lower than those of mesic rodents (McNab & Morrison, 1963; Nevo & Shkolnik, 1974; Haim & Borut, 1981; Goyal, Ghosh & Prakash, 1981; Haim & Fairall, 1986; Webb & Skinner, 1996). This was not the case for the BMRs of the *Rhabdomys* populations observed in this study. Despite the clinal decrease in BMR, inversely related to the aridity gradient, the BMR's of rodents from arid zones were not significantly lower than those of rodents from mesic zones. The failure to discern clear arid-mesic differences in the BMRs of the rodents in this study, may be a consequence of ENSO-related resource unpredictability in the mesic zones, mimicking, to a certain degree, the selection pressures on BMR in arid zones. Alternatively, the lack of significant geographical variation of BMR between sites in this study may be due to the variation in BMR within sites, a factor less important in the linear regression of rainfall unpredictability and BMR.

The DEE of animals from the different regions remains the best indicator of geographic variation in energy conservatism and therefore the most conclusive finding of this study. At both thermoneutrality and under conditions of cold stress, the geographic variation in the DEE of the animals was explained by Model 2 when the selection effects of both aridity stresses and ENSO-related rainfall unpredictability were taken into account. Thus, it can be concluded that conservative energetic traits have evolved in both the arid and the ENSO-affected zones of southern Africa, in response to the stresses associated with the unpredictable habitat productivity in these areas.

In this study it was also shown that the geographic variation in the proximate responses of DEE and T_b to conditions of cold stress conformed well with the predictions of Model 2. This indicates that the proximate responses of the physiological

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traits of R. *pumilio* are generated by a suite of ultimate responses that have also evolved in response to the selection pressures of both aridity and ENSO-related rainfall unpredictability. In other words, in addition to possessing conservative energetic traits, animals from arid and ENSO-zones are characterised by less energetically expensive thermoregulatory responses than animals from regions subject to less severe aridity and ENSO-related stresses.

In conclusion, the physiological traits and proximate responses of R. *pumilio*, seem to be synonymous in both the arid regions and the ENSO-afflicted regions of southern Africa. Although unpredictable periods of low habitat productivity generated by ENSO-related droughts occur less frequently in non-desert ENSO zones, they are clearly of sufficient magnitude to mimic the selection pressures of rainfall unpredictability in arid zones.

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Table 1: Mean minimum and mean maximum temperatures in mid Summer and mid Winter for six geographical sites across southern Africa. Months were chosen as the highest mean maximum for Summer and the lowest mean minimum for Winter (CCWR, 1998).

	Summer				Winter			
	Month	Max (°C)	Min (°C)	Range (°C)	Month	Max (°C)	Min (°C)	Range (°C)
Goageb	Dec.	34.9	20.2	14.7	July	22.0	2.3	19.7
Aus	Jan.	21.4	14.1	7.3	Aug.	17.2	10.3	6.9
Keetmanshoop	Jan.	34.8	17.6	17.2	July	21.3	5.2	16.1
Rietfontein	Jan.	35.8	19.7	6.1	July	21.8	1.2	20.6
Vanzylsrus	Jan.	36.0	18.9	7.1	Aug.	24.6	3.5	21.1
Potchefstroom	Jan.	29.2	16.2	13.0	July	21.8	1.2	20.6

Table 2: The mean ± SD (n = 5) body mass, lower critical limit of thermoneutrality (T_{lc}), BMR and minimum wet thermal conductance of *R. pumilio* from six geographical sites in southern Africa.

	Mass (g)	± SD	T_{lc} (°C)	± SD	BMR (ml O_2/g/h)	± SD	Conductance (mlO_2/g/h/°C)	± SD
Goageb	57.21	6.41	32.54	2.44	0.739	0.072	0.111	0.017
Aus	57.88	5.84	31.38	0.87	0.788	0.074	0.095	0.011
Keetmanshoop	54.24	5.51	30.15	2.66	0.825	0.124	0.113	0.013
Rietfontein	53.48	4.74	30.12	2.15	0.834	0.083	0.126	0.031
Vanzylsrus	51.81	6.13	30.84	1.32	0.846	0.076	0.117	0.024
Potchefstoom	55.96	2.93	28.55	1.71	0.884	0.076	0.096	0.013

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Table 3: The mean ± SD (n = 5) body temperature of *R. pumilio* from six geographical sites in southern Africa for selected circadian time phases at an ambient temperature of 30°C.

	24 hour* (°C)	± SD	Night* (°C)	± SD	Day* (°C)	± SD	am* (°C)	± SD	pm* (°C)	± SD
Goageb	36.41	0.21	36.09	0.18	36.69	0.36	36.51	0.38	36.89	0.42
Aus	36.91	0.29	37.02	0.36	36.78	0.42	36.63	0.42	36.97	0.38
Keetmanshoop	36.69	0.43	36.74	0.45	36.61	0.49	36.78	0.41	36.69	0.45
Rietfontein	36.89	0.58	37.35	0.65	37.49	0.45	37.35	0.65	37.61	0.47
Vanzylsrus	36.61	0.41	36.71	0.62	36.82	0.38	36.77	0.54	37.13	0.36
Potchefstroom	36.89	0.56	36.74	0.78	37.04	0.41	36.72	0.41	37.32	0.47

* **24 hour:** 12h00 - 12h00 **Night:** 18h00 - 6h00 **Day:** 6h00 - 18h00 **am:** 6h00 - 12h00 **pm:** 12h00 - 18h00

Table 4: The mean ± SD (n = 5) body temperature of *R. pumilio* from six geographical sites in southern Africa for selected circadian phases at an ambient temperature of 20°C.

	24 hour* (°C)	± SD	Night* (°C)	± SD	Day* (°C)	± SD	am* (°C)	± SD	pm* (°C)	± SD
Goageb	36.15	0.21	36.03	0.18	36.86	0.42	36.71	0.42	36.63	0.49
Aus	36.05	0.63	36.11	0.51	36.14	0.65	35.47	1.11	36.51	0.80
Keetmanshoop	35.78	0.31	35.83	0.51	35.91	0.83	35.59	0.65	36.43	0.83
Rietfontein	36.53	0.56	36.69	0.61	36.75	0.76	36.41	0.94	36.82	0.87
Vanzylsrus	36.48	0.85	36.16	0.65	36.81	1.21	36.48	1.21	37.07	1.00
Potchefstroom	35.83	0.98	35.57	1.14	36.08	0.85	35.72	0.61	36.41	1.20

* **24 hour:** 12h00 - 12h00 **Night:** 18h00 - 6h00 **Day:** 6h00 - 18h00 **am:** 6h00 - 12h00 **pm:** 12h00 - 18h00

Table 5: The mean ± SD (n = 5) energy expenditure (kJ) of *R. pumilio* from six geographical sites in southern Africa for selected circadian phases at an ambient temperature of 30°C.

	24 hour* (kJ)	± SD	Night* (kJ)	± SD	Day* (kJ)	± SD	am* (kJ)	± SD	pm* (kJ)	± SD
Goageb	34.46	6.06	16.13	2.77	17.41	2.59	8.50	1.57	9.27	1.11
Aus	36.97	6.19	19.35	2.66	17.64	3.93	11.03	3.99	9.20	1.64
Keetmanshoop	36.99	6.89	16.18	2.21	20.70	5.45	10.11	2.96	10.49	2.75
Rietfontein	37.69	3.75	18.54	2.07	19.06	2.83	9.27	1.11	9.69	1.86
Vanzylsrus	26.83	4.12	13.11	2.55	13.86	1.99	6.53	1.02	7.55	0.96
Potchefstroom	33.21	2.96	15.81	2.02	17.37	2.55	7.67	1.96	9.77	0.69

* 24 hour: 12h00 - 12h00   Night: 18h00 - 6h00   Day: 6h00 - 18h00   am: 6h00 - 12h00   pm: 12h00 - 18h00

Table 6: The mean ± SD (n = 5) energy expenditure (kJ) of *R. pumilio* from six geographical sites in southern Africa for selected circadian phases at an ambient temperature of 20°C.

	24 hour* (kJ)	± SD	Night* (kJ)	± SD	Day* (kJ)	± SD	am* (kJ)	± SD	pm* (kJ)	± SD
Goageb	51.00	11.31	24.49	6.41	24.39	6.58	12.18	3.31	12.48	4.07
Aus	62.69	7.89	31.55	4.64	30.27	3.93	14.33	1.75	15.87	2.13
Keetmanshoop	62.58	5.23	30.89	1.78	31.60	3.93	14.93	2.24	16.71	2.05
Rietfontein	73.04	7.11	37.06	3.75	35.99	3.47	17.57	1.83	18.43	2.07
Vanzylsrus	60.46	12.18	29.67	5.60	30.85	6.65	14.85	3.37	14.64	2.35
Potchefstroom	54.85	6.23	26.23	3.01	28.64	3.61	13.52	2.07	14.98	1.51

* 24 hour: 12h00 - 12h00   Night: 18h00 - 6h00   Day: 6h00 - 18h00   am: 6h00 - 12h00   pm: 12h00 - 18h00

Table 7: Comparisons of day and night body temperature, day and night energy expenditure, evening and morning body temperature, and evening and morning energy expenditure, of *R. pumilio* (n = 30) at T_a = 30°C and T_a = 20°C (Wilcoxan signed rank tests).

	T_b (°C)				Energy expend. (kJ)			
	z	p	ΔT_b	± SD	z	p	Δ kJ	± SD
$T_a = 30°C$								
day* - night*	2.41	<0.05	0.47	0.49	1.56	>0.05	1.15	3.41
pm* - am*	3.88	<0.05	0.32	0.36	2.20	<0.05	0.49	1.83
$T_a = 20°C$								
day* - night*	3.20	<0.05	0.40	0.73	0.51	>0.05	0.33	2.24
pm* - am*	4.44	<0.05	0.77	0.63	3.70	<0.05	1.16	1.66

* **Night:** 18h00 - 6h00 **Day:** 6h00 - 18h00 **am:** 6h00 - 12h00 **pm:** 12h00 - 18h00

Table 8: The change in the mean ± SD (n = 5) body temperature of *R. pumilio* from six geographical sites in southern Africa as a function of ambient temperature.

	30°C	± SD	20°C	± SD	ΔT_b (°C)	± SD
Goageb	36.41	0.21	36.15	0.21	-0.61	0.04
Aus	36.91	0.29	36.05	0.63	-0.92	0.31
Keetmanshoop	36.69	0.43	35.78	0.31	-0.60	0.36
Rietfontein	36.89	0.58	36.53	0.56	-0.45	0.42
Vanzylsrus	36.61	0.41	36.48	0.85	-0.56	0.34
Potchefstroom	36.89	0.56	35.83	0.98	-1.17	0.97

Table 9: The change in the mean ± SD (n = 5) energy expenditure of *R. pumilio* from six geographical sites in southern Africa as a function of ambient temperature.

	30°C	± SD	20°C	± SD	ΔDEE(kJ)	± SD
Goageb	34.46	6.06	51.00	11.31	16.538	12.396
Aus	36.97	6.19	62.69	7.89	25.714	2.831
Keetmanshoop	36.99	6.89	62.58	5.23	25.590	2.790
Rietfontein	37.69	3.75	73.04	7.11	35.357	5.682
Vanzylsrus	26.83	4.12	60.46	12.18	33.623	9.290
Potchefstroom	33.21	2.96	54.85	6.23	21.639	4.062

Table 10: The mean ± SD (n = 5) minimum body temperature of *R. pumilio* from six geographical sites in southern Africa at $T_a = 30°C$ and $T_a = 20°C$.

	30°C		20°C	
	$T_b$min (°C)	± SD	$T_b$min (°C)	± SD
Goageb	35.23	0.17	34.78	0.37
Aus	35.34	0.45	34.56	0.67
Keetmanshoop	35.75	0.66	34.13	0.26
Rietfontein	35.70	0.81	34.78	0.70
Vanzylsrus	35.34	0.53	34.76	1.06
Potchefstroom	35.94	0.67	34.41	1.22

Table 11: The mean ± SD (n = 5) circadian amplitudes of body temperature and oxygen consumption of *R. pumilio* from six geographical sites in southern Africa at $T_a = 30°C$ and $T_a = 20°C$.

	30 °C		20 °C		30 °C		20 °C	
	R_t(°C)	± SD	R_t(°C)	± SD	R_{vo_2} (mlO$_2$/g/h)	± SD	R_{vo_2} (mlO$_2$/g/h)	± SD
Goageb	2.47	0.19	2.79	0.37	1.295	0.338	1.656	0.521
Aus	2.67	0.59	3.03	0.29	1.258	0.316	1.642	0.404
Keetmanshoop	1.84	0.89	3.07	0.59	1.655	0.135	1.735	0.275
Rietfontein	2.95	0.44	3.40	0.61	1.557	0.364	2.087	0.589
Vanzylsrus	2.95	0.93	3.14	0.86	1.079	0.286	1.617	0.443
Potchefstroom	2.23	0.45	3.01	1.16	1.480	0.393	1.580	0.378
Mean	2.52	0.71	3.07	0.67	1.387	0.349	1.792	0.441

Table 12: Comparisons of physiological traits of *R.pumilio* (n = 30) at an ambient temperature of 30°C and an ambient temperature of 20°C (Wilcoxan signed rank tests).

	z	p	
T_b	4.56	<0.01	$T_a=30°C > T_a=20°C$
DEE	4.79	<0.01	$T_a=30°C < T_a=20°C$
$T_{b\ min}$	4.46	<0.01	$T_a=30°C > T_a=20°C$
R_t	2.40	<0.05	$T_a=30°C < T_a=20°C$
R_{vo_2}	3.06	<0.01	$T_a=30°C < T_a=20°C$

Table 13: Results of Kruskal-Wallis tests for geographic differences in physiological traits and phenotypic responses of *R. pumilio*.

	H-statistic	p
BMR	8.435	>0.05
C_{min}	9.542	>0.05
$T_{b\,min}$ @ 30°C	5.568	>0.05
$T_{b\,min}$ @ 20°C	5.455	>0.05
mean T_b @ 30°C	11.193	<0.05*
meanT_b @ 20°C	5.604	>0.05
DEE @ 30°C	11.534	<0.05*
DEE @ 20°C	13.092	<0.05*
R_t @ 30°C	8.479	>0.05
R_t @ 20°C	3.276	>0.05
Rvo_2 @ 30°C	9.785	>0.05
Rvo_2 @ 20°C	2.863	>0.05
ΔT_b	11.217	<0.05*
ΔDEE	13.451	<0.05*

*denotes significant differences

Table 14: Results of first and second order regressions fitted to physiological traits and phenotypic responses of *R. pumilio* from six geographical sites in southern Africa as a function of the co-efficient of variation of rainfall.

	1st order		2nd order	
	r^2	p	r^2	p
BMR	0.2771	<0.05*	0.2844	<0.05*
C_{min}	0.0006	>0.05	0.0452	>0.05
$T_{b\ min}$ @ 30°C	0.0691	>0.05	0.0727	>0.05
$T_{b\ min}$ @ 20°C	0.0007	>0.05	0.0041	>0.05
mean T_b @ 30°C	0.1376	<0.05*	0.1979	<0.05*
mean T_b @ 20°C	0.0015	>0.05	0.0136	>0.05
DEE @ 30°C	0.1033	>0.05	0.1564	<0.05*
DEE @ 20°C	0.1034	>0.05	0.3721	<0.05*
R_t @ 30°C	0.0077	>0.05	0.0175	>0.05
R_t @ 20°C	0.0167	>0.05	0.0589	>0.05
R_{vo_2} @ 30°C	0.0002	>0.05	0.0261	>0.05
R_{vo_2} @ 20°C	0.0011	>0.05	0.0562	>0.05
ΔT_b	0.1615	<0.05*	0.1781	<0.05*
ΔDEE	0.1044	>0.05	0.3968	<0.05*

*denotes significant differences
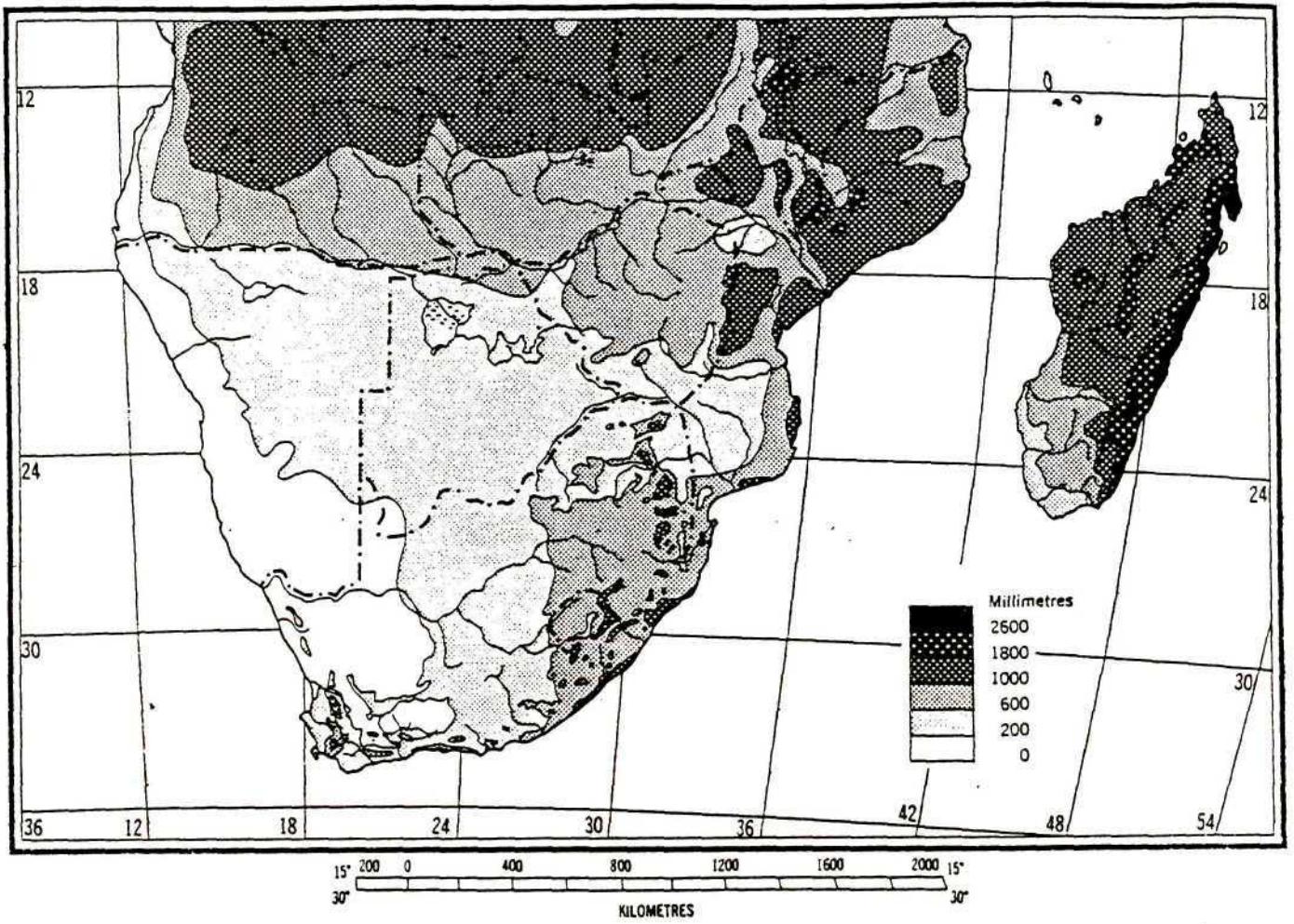
Fig. 1: Map of mean annual rainfall regions in southern Africa (Tyson, 1986). Mean annual rainfall increases from west to east across southern Africa, representing an aridity gradient.

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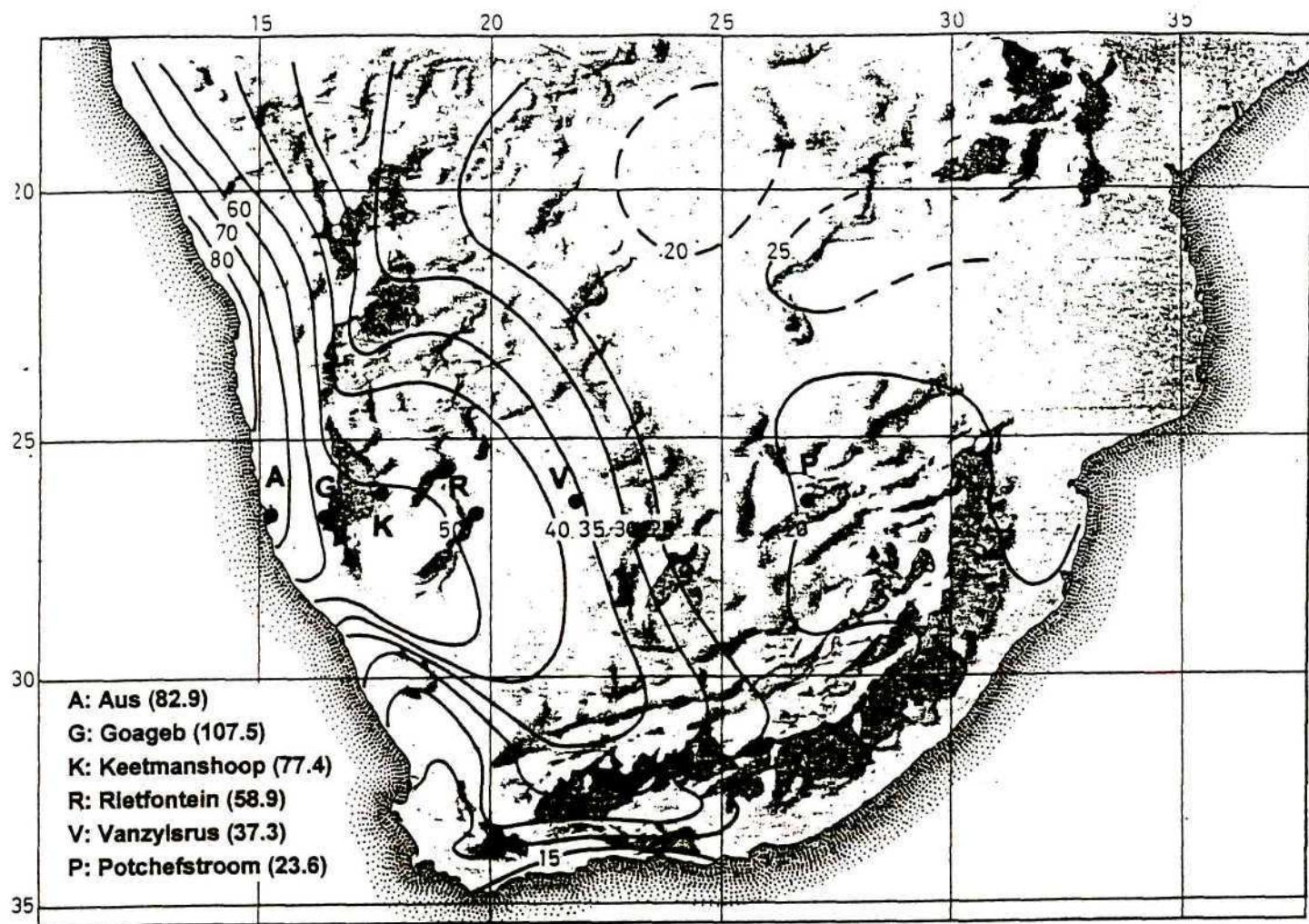
Fig. 2: Variability of rainfall, representing an aridity gradient across southern Africa (Schulze, 1966). Isohyets represent the co-efficient of variation of mean annual rainfall (CV) expressed as a percentage. Bracketed numbers represent the CV of rainfall of the specific sites from which rodents were sampled in this study. Variability calculated with respect to regional values of rainfall is less that that calculated from data of a single rainfall station.

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Type I ENSO Generalized Drought Precursor Pattern
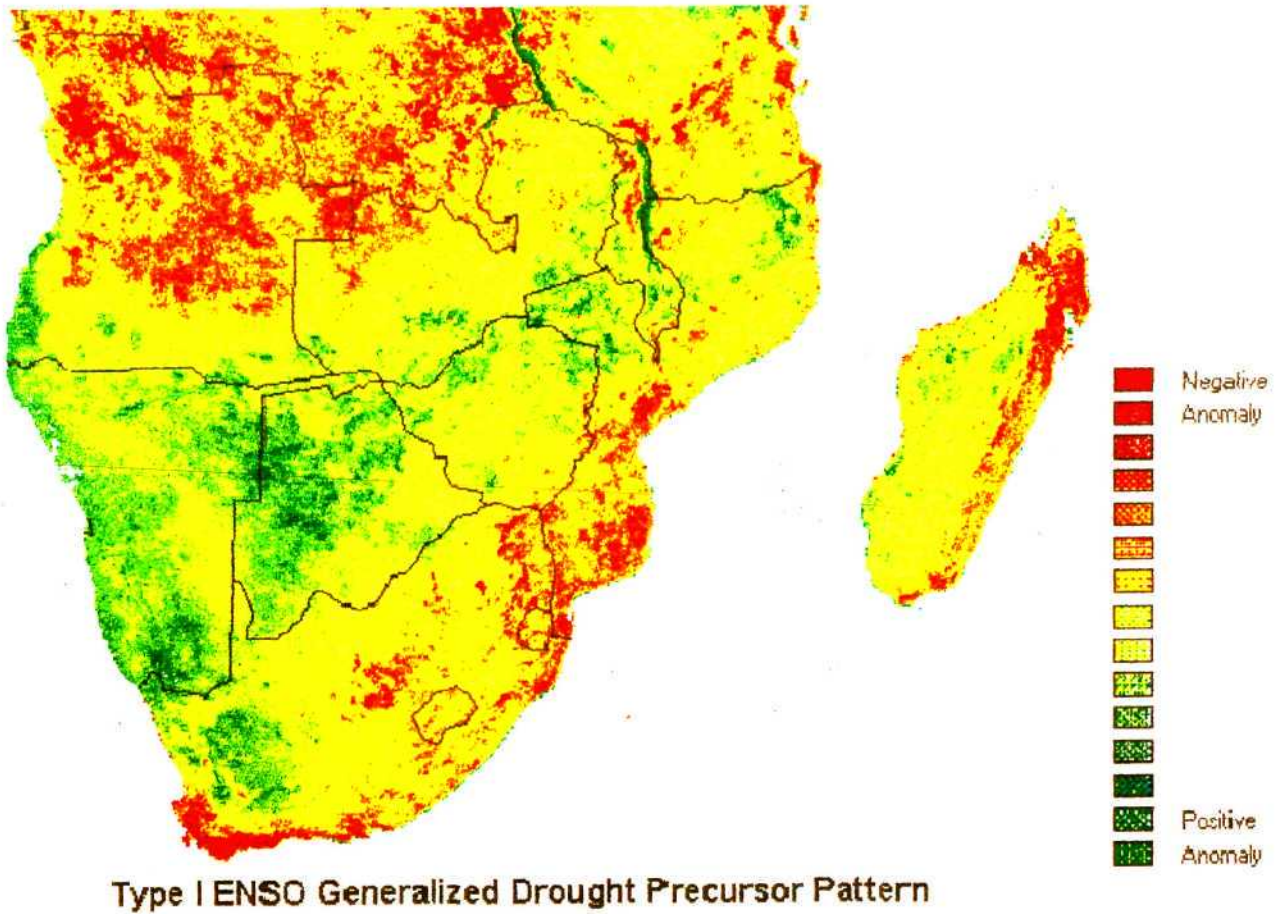
Fig. 3: Map of southern Africa showing generalised rainfall anomalies of areas during El Niño Southern Oscillation events. The eastern regions of southern Africa experience negative rainfall anomalies during El Niño periods. **Source**: Clark Labs ENSO Monitor, 1998 (http://www.idrisi.clarku.edu/10applic/assaf1/monitorcont.htm).
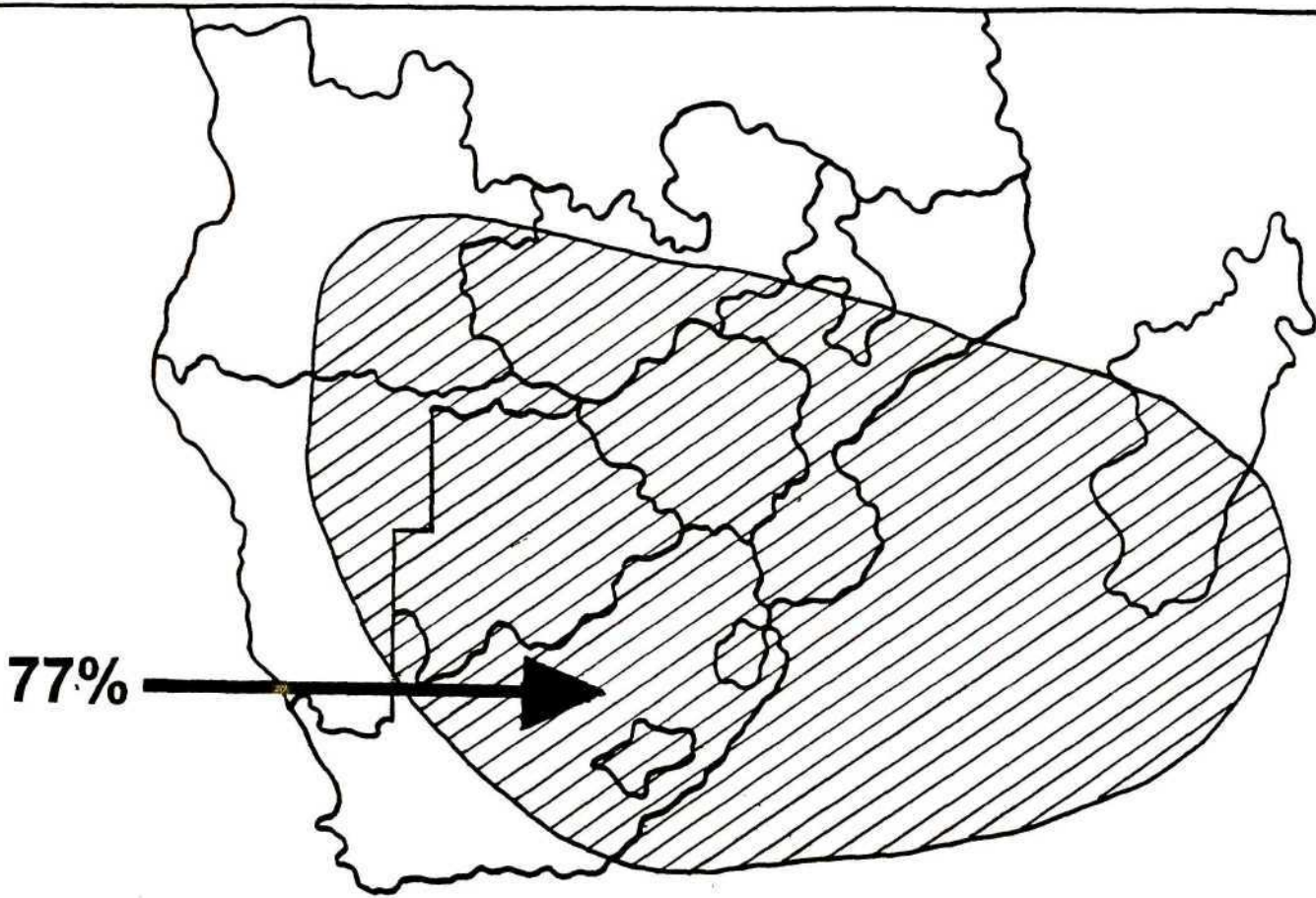
Fig. 4: Map of southern Africa. The shaded area represents regions affected by past El Niño Southern Oscillation events. The percentage of the normal mean annual rainfall experienced in this area, during El Niño years, is given. **Redrawn from**: Clark Labs ENSO Monitor, 1998 (http://www.idrisi.clarku.edu/10applic/assaf1/monitorcont.htm).
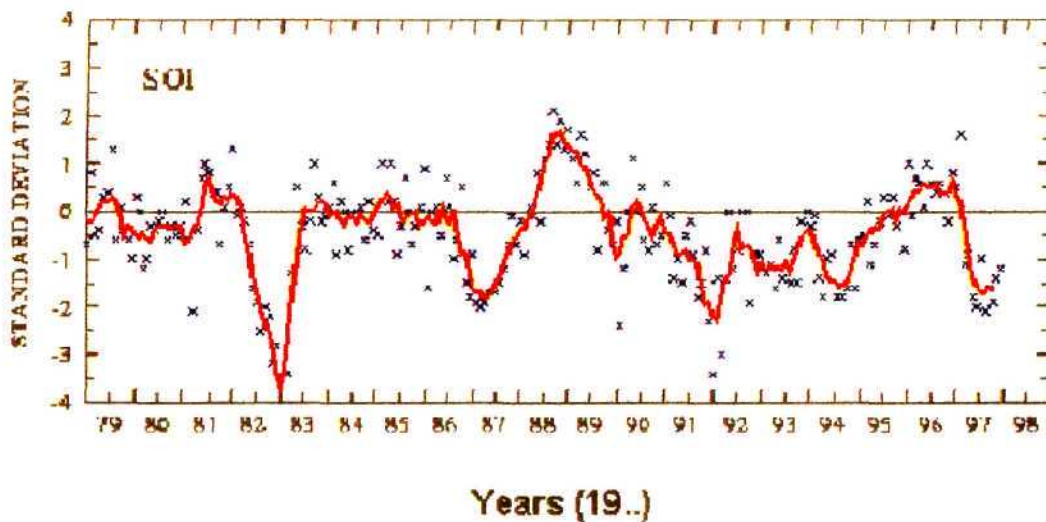
Fig. 5: A plot of the Southern Oscillation Index (SOI) between 1979-1998. Each ENSO event is represented by a major trough below the normal line. Peaks above the normal line represent La Niña events. **Source**: Clark Labs ENSO Monitor, 1998 (http://www.idrisi.clarku.edu/10applic/assaf1/monitorcont.htm).
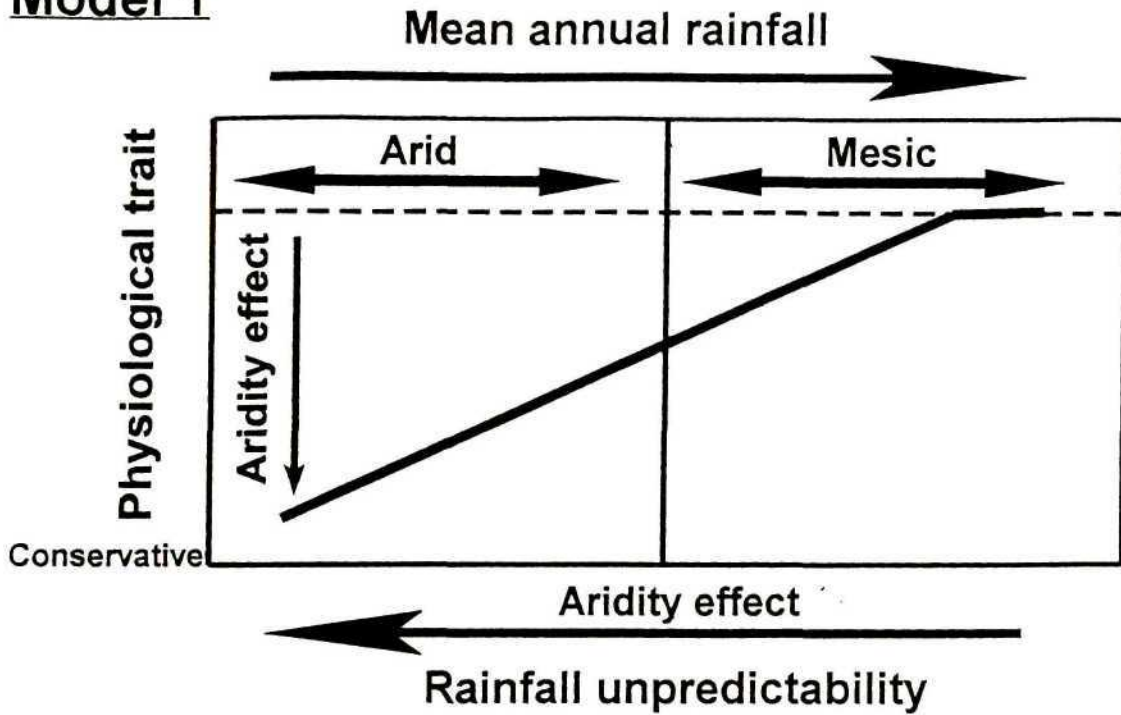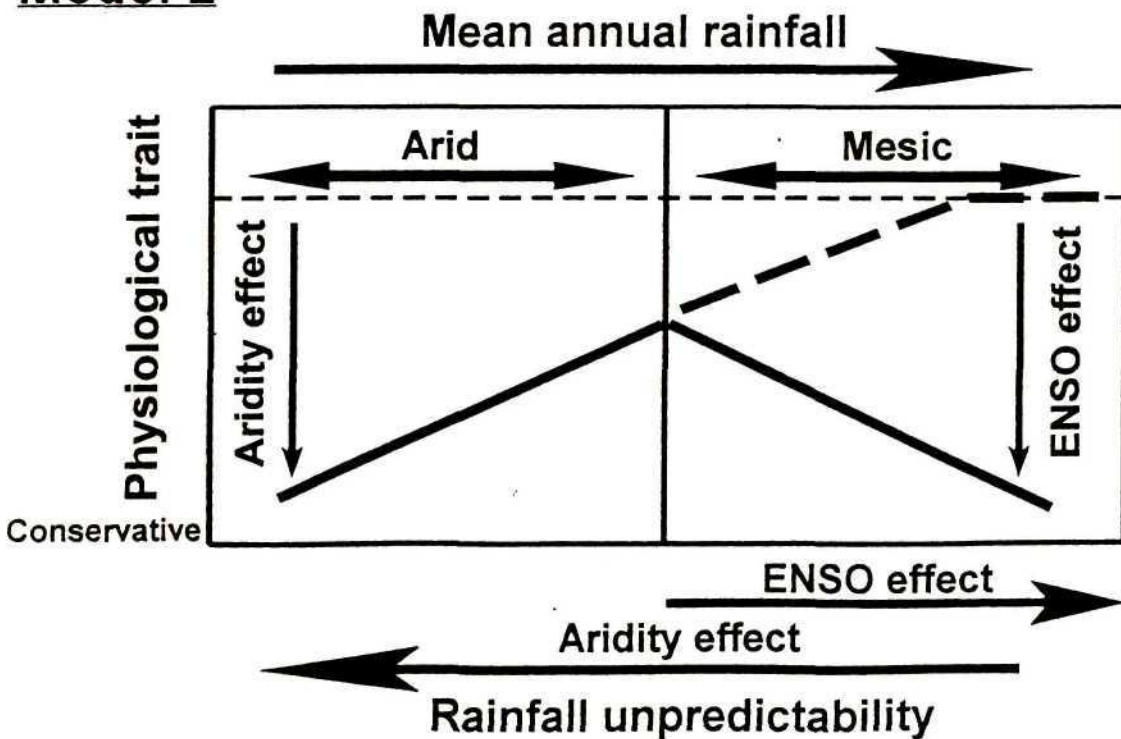
Fig. 6: Diagrammatic representation of models to be tested. Model 1 predicts increasing conservatism of metabolic parameters (e.g. BMR) with increasing aridity. Model 2, in addition to the prediction of Model 1, predicts evidence of conservatism of metabolic parameters in the ENSO-afflicted regions in the higher rainfall sites.
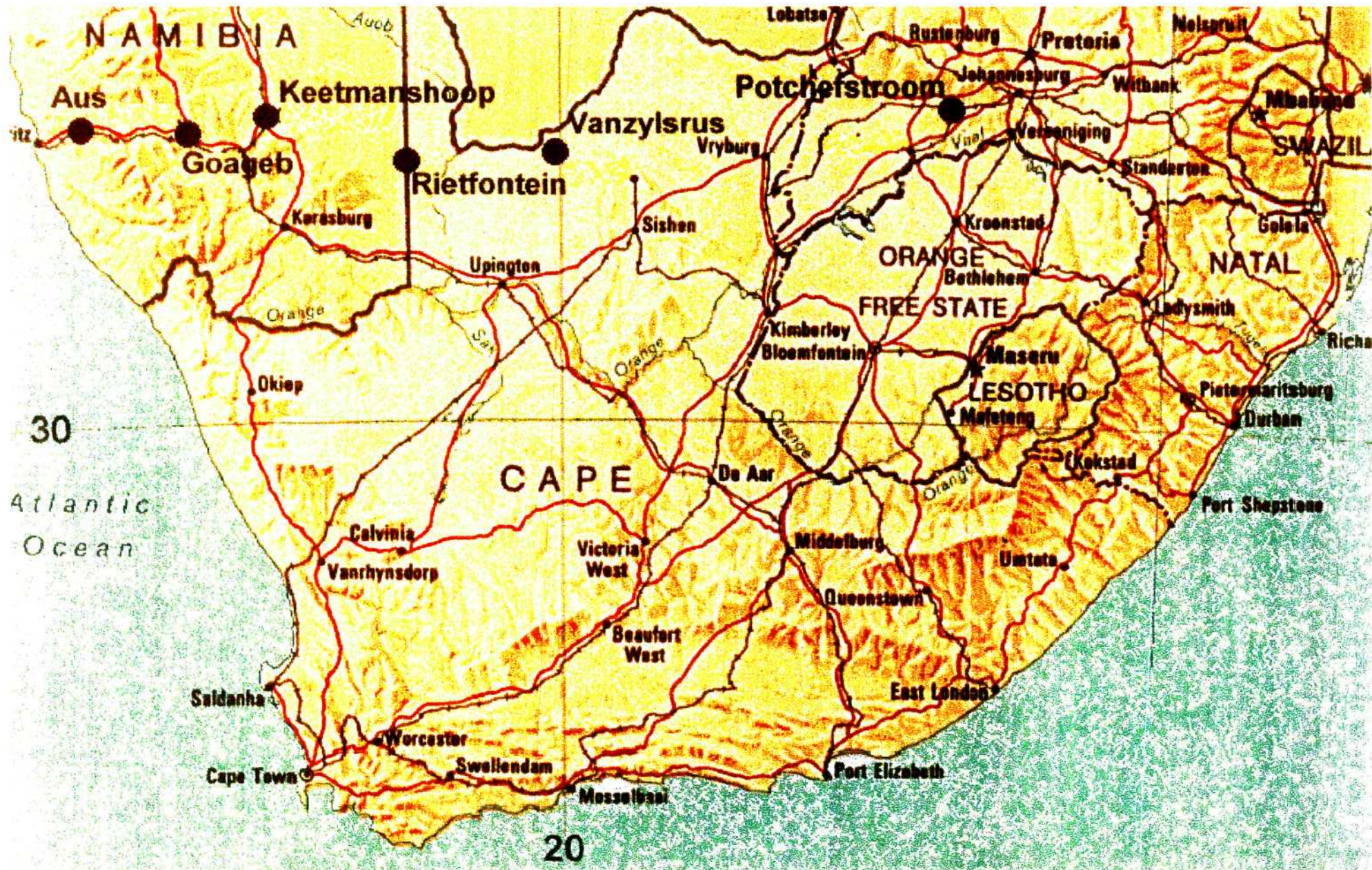
Fig. 7: Map of southern Africa. Sites from which *R. pumilio* were collected are represented by ●
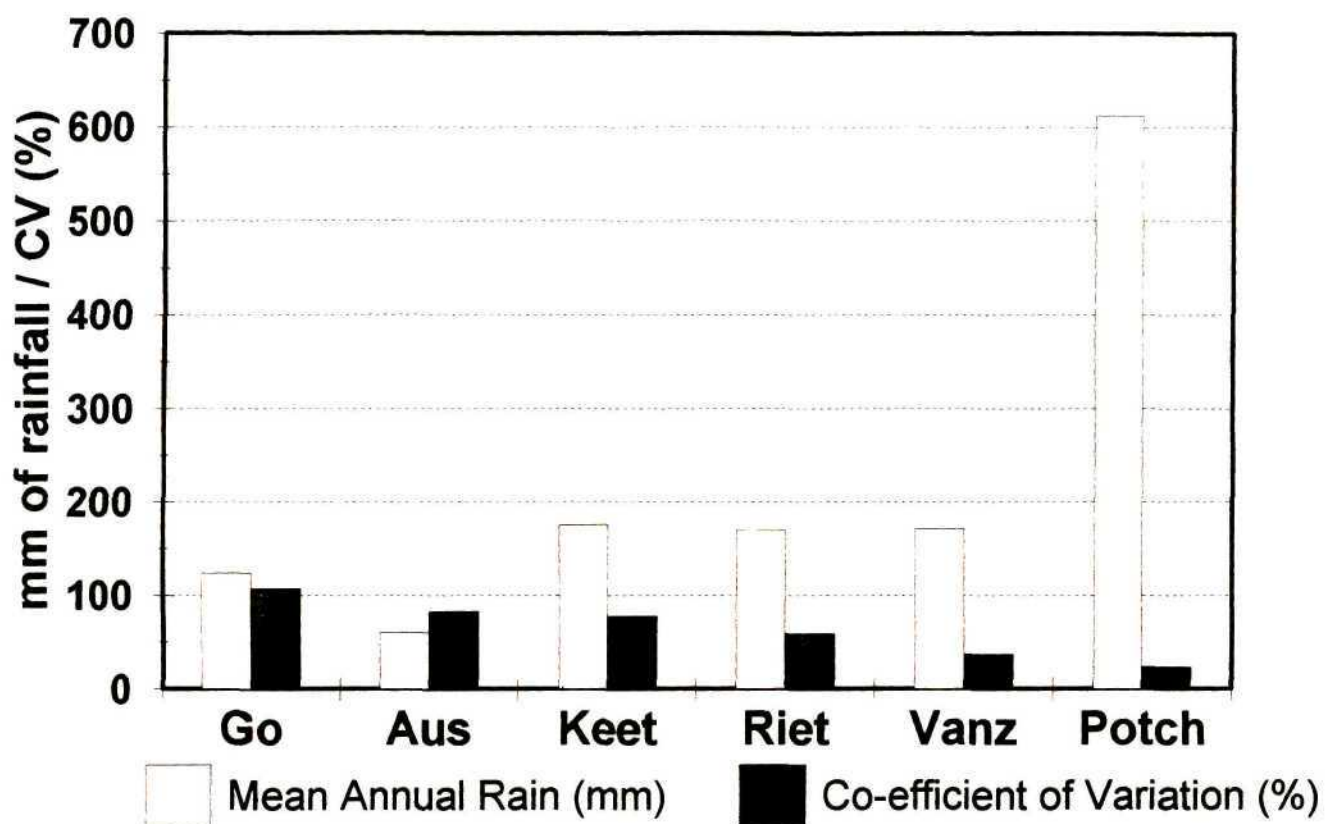
Fig. 8: Mean annual rainfall (mm) and co-efficient of variation of mean annual rainfall of sites from which study animals were collected. Data courtesy of the Computing Centre for Water Research, University of Natal (1997).

Fig. 9: Oxygen consumption (ml O_2/g/h) of thirty striped-field mice *Rhabdomys pumilio* from six geographical regions across southern Africa, as a function of ambient temperature (°C).
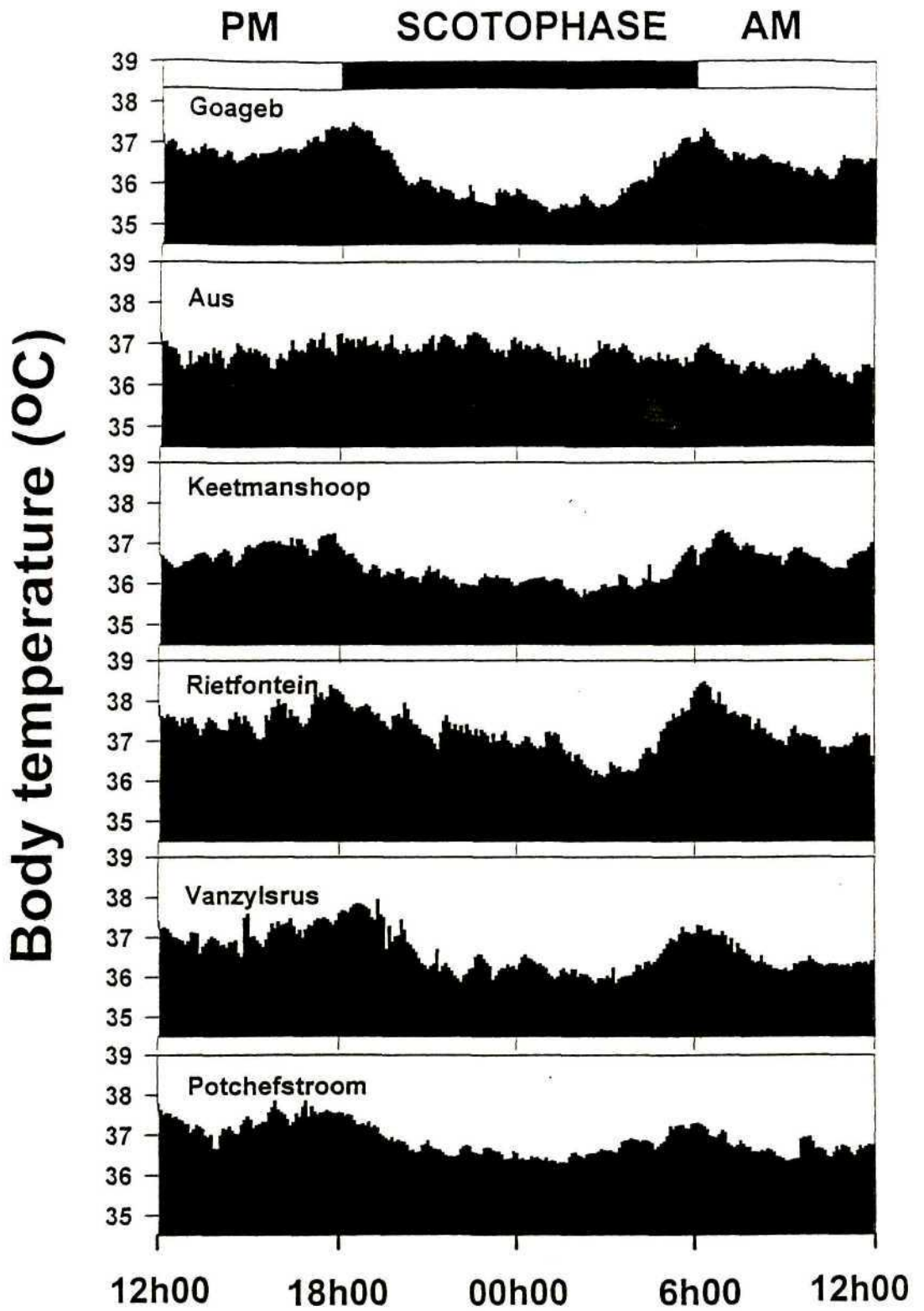
Fig. 10: Circadian rhythms of body temperature (°C) at T_a = 30 °C, averaged for five rodents (*Rhabdomys pumilio*) from each study site.

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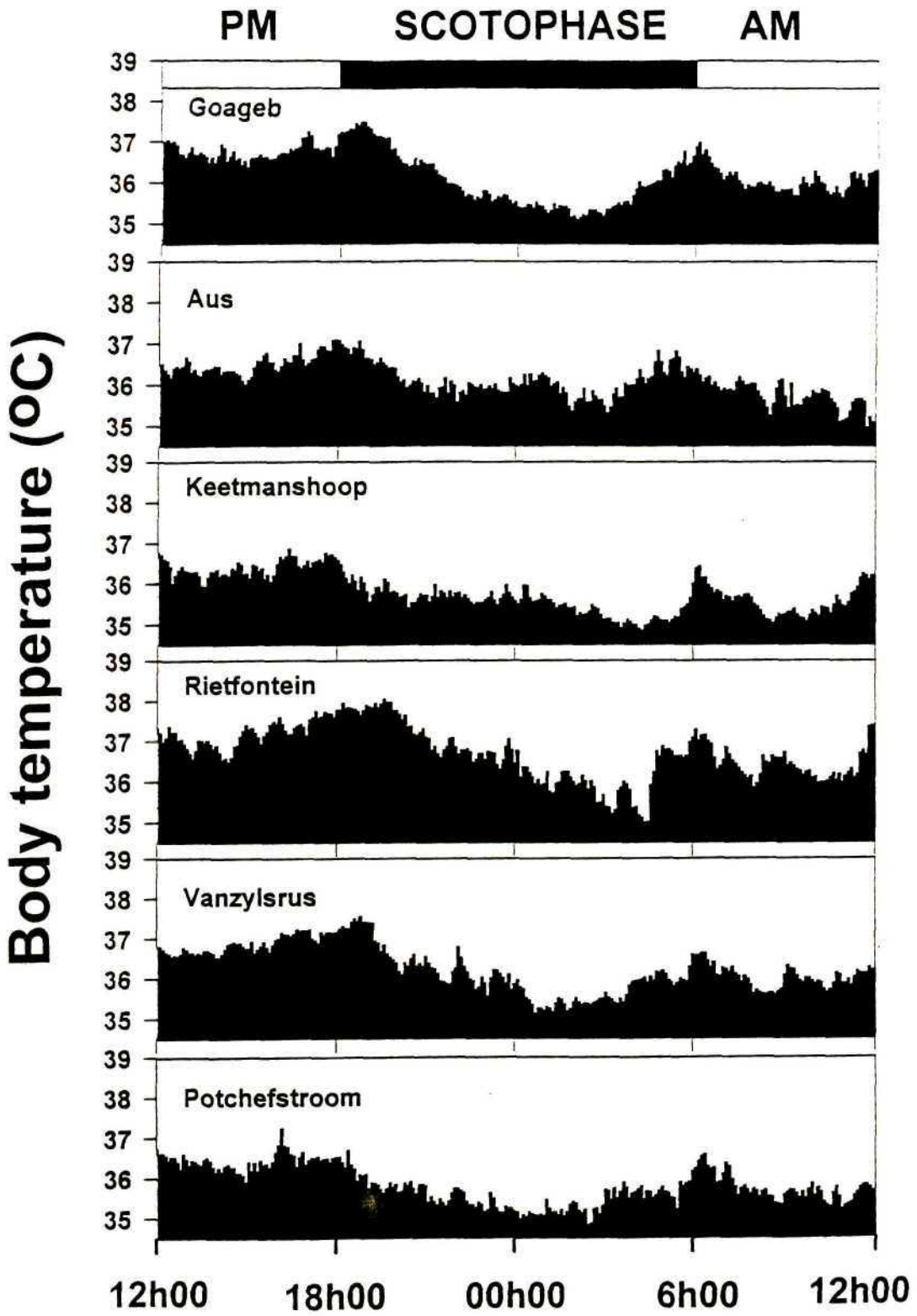
Fig. 11: Circadian rhythms of body temperature (°C) at $T_a = 20$°C, averaged for five rodents (*Rhabdomys pumilio*) from each study site.
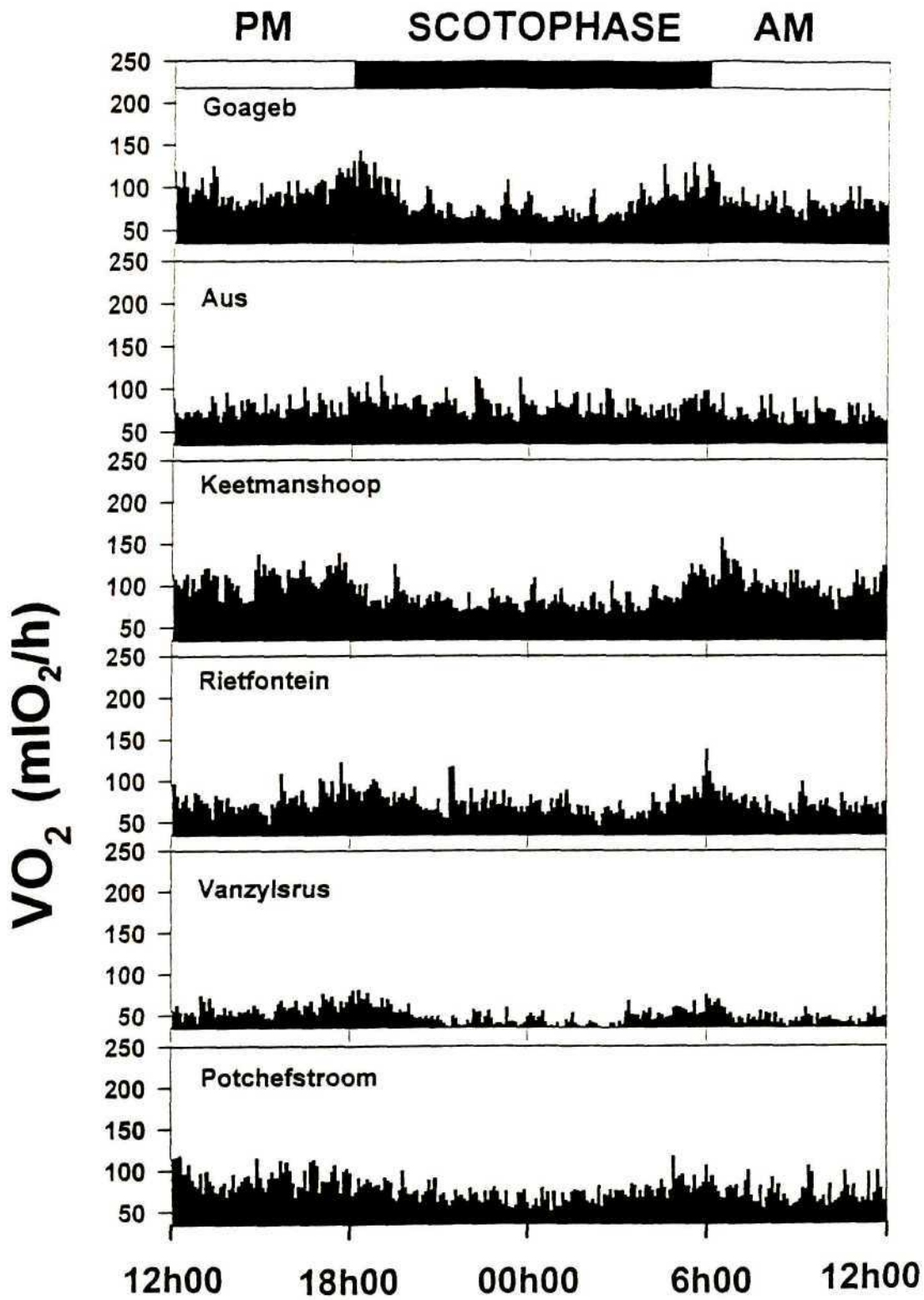
Fig. 12: Circadian rhythms of oxygen consumption (mlO$_2$/h) at T$_a$ = 30°C, averaged for five rodents (*Rhabdomys pumilio*) from each study site.

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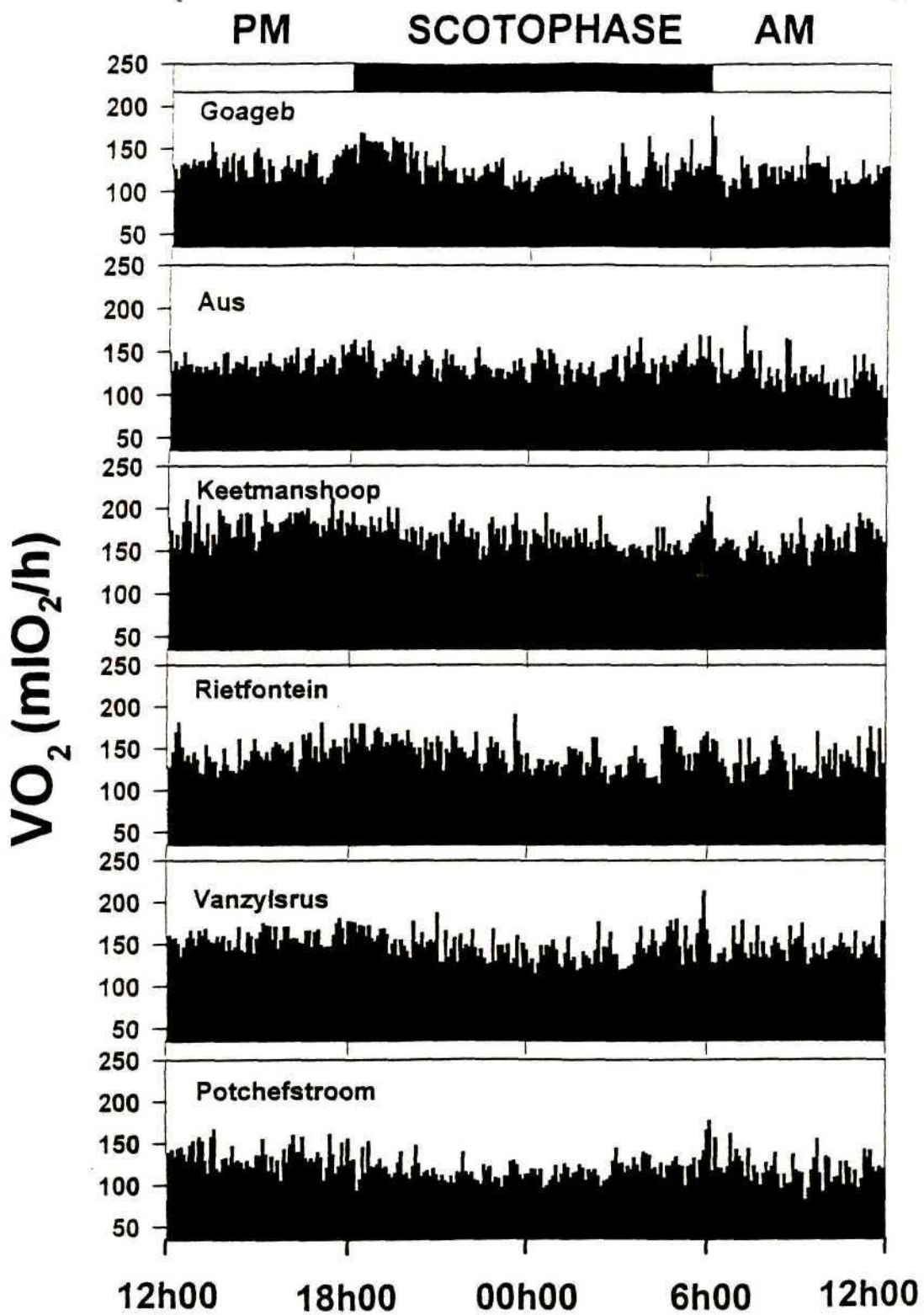
Fig. 13: Circadian rhythms of oxygen consumption (mlO_2/h) at $T_a = 20°C$, averaged for five rodents (*Rhabdomys pumilio*) from each study site.
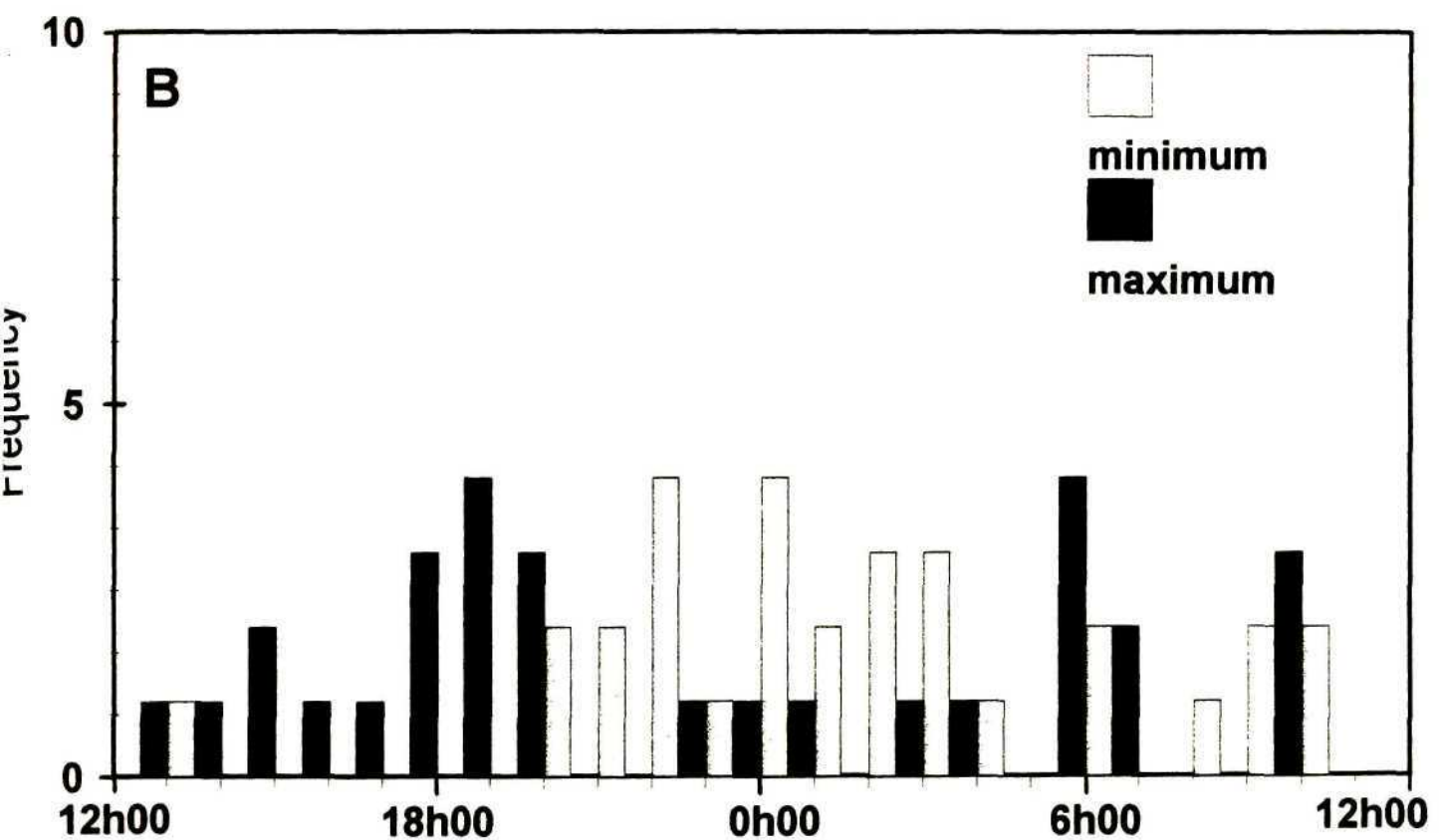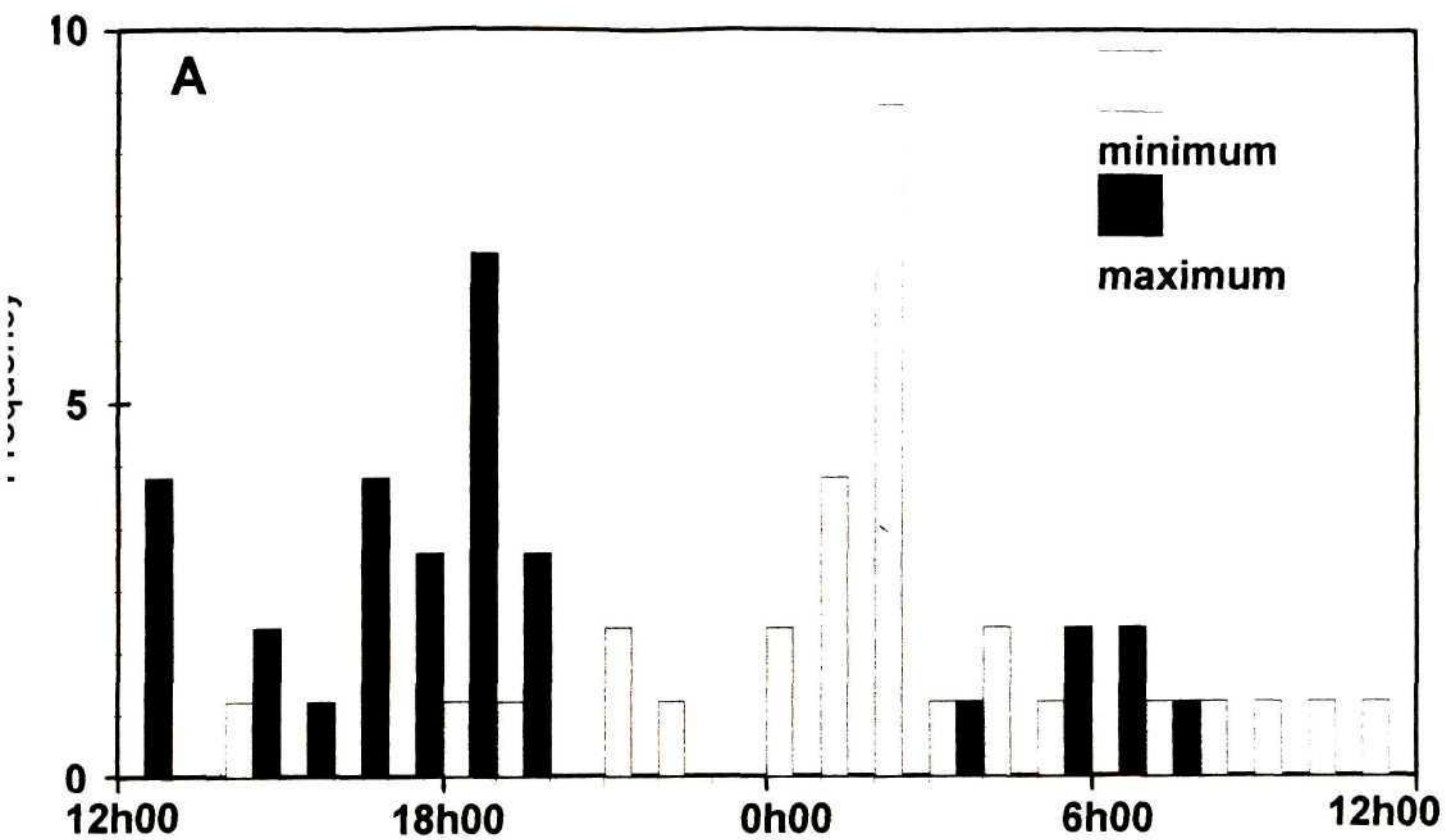
Fig. 14: Frequency of occurrence of minimum and maximum of a) body temperatures and
b) rates of oxygen consumption of thirty rodents (*Rhabdomys pumilio*) during each hourly
circadian interval. The ambient temperature was 30°C.
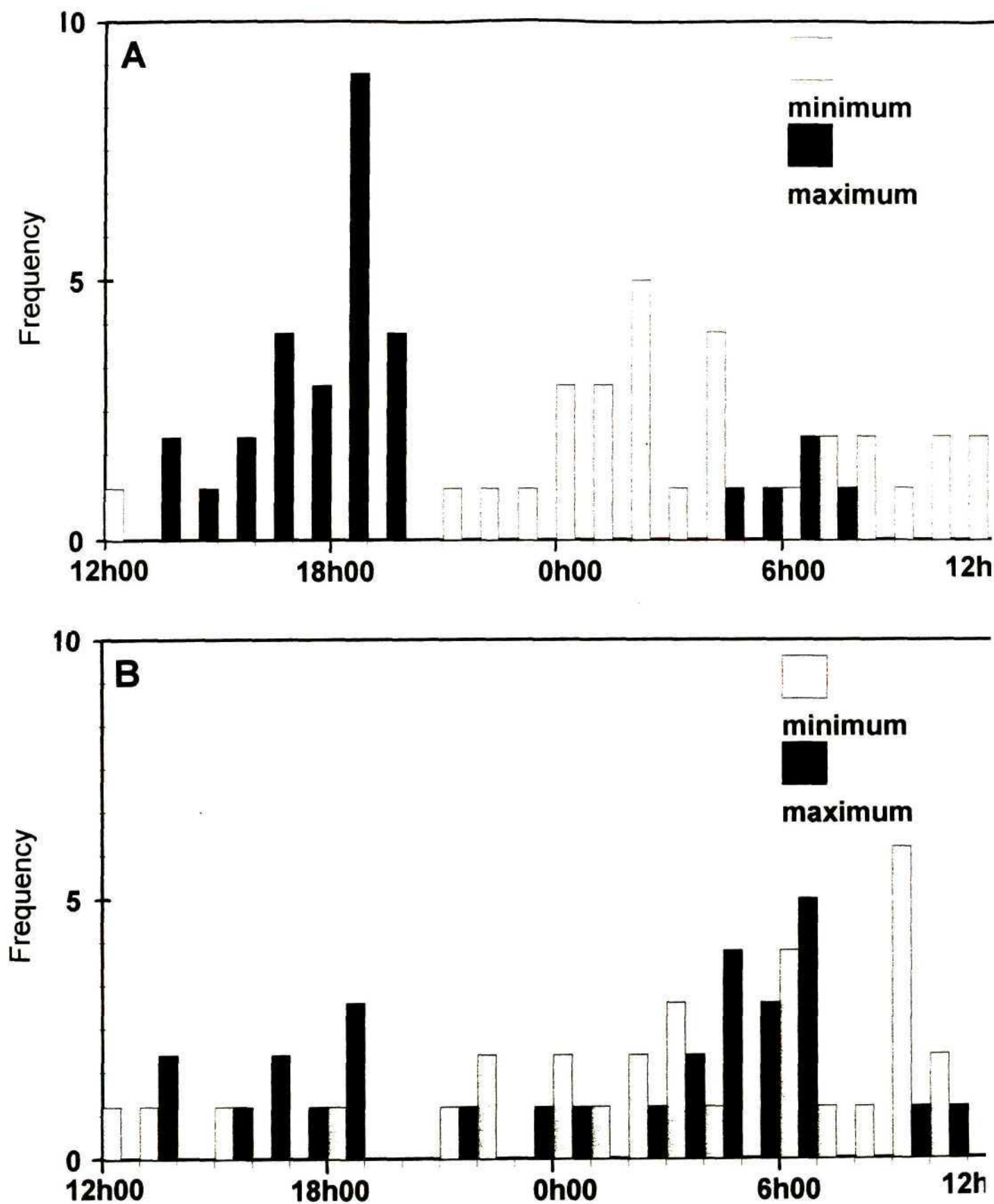
Fig. 15: Frequency of occurrence of minimum and maximum of a) body temperatures and
b) rates of oxygen consumption of thirty rodents (*Rhabdomys pumilio)* during each hourly
circadian interval. The ambient temperature was 20°C.
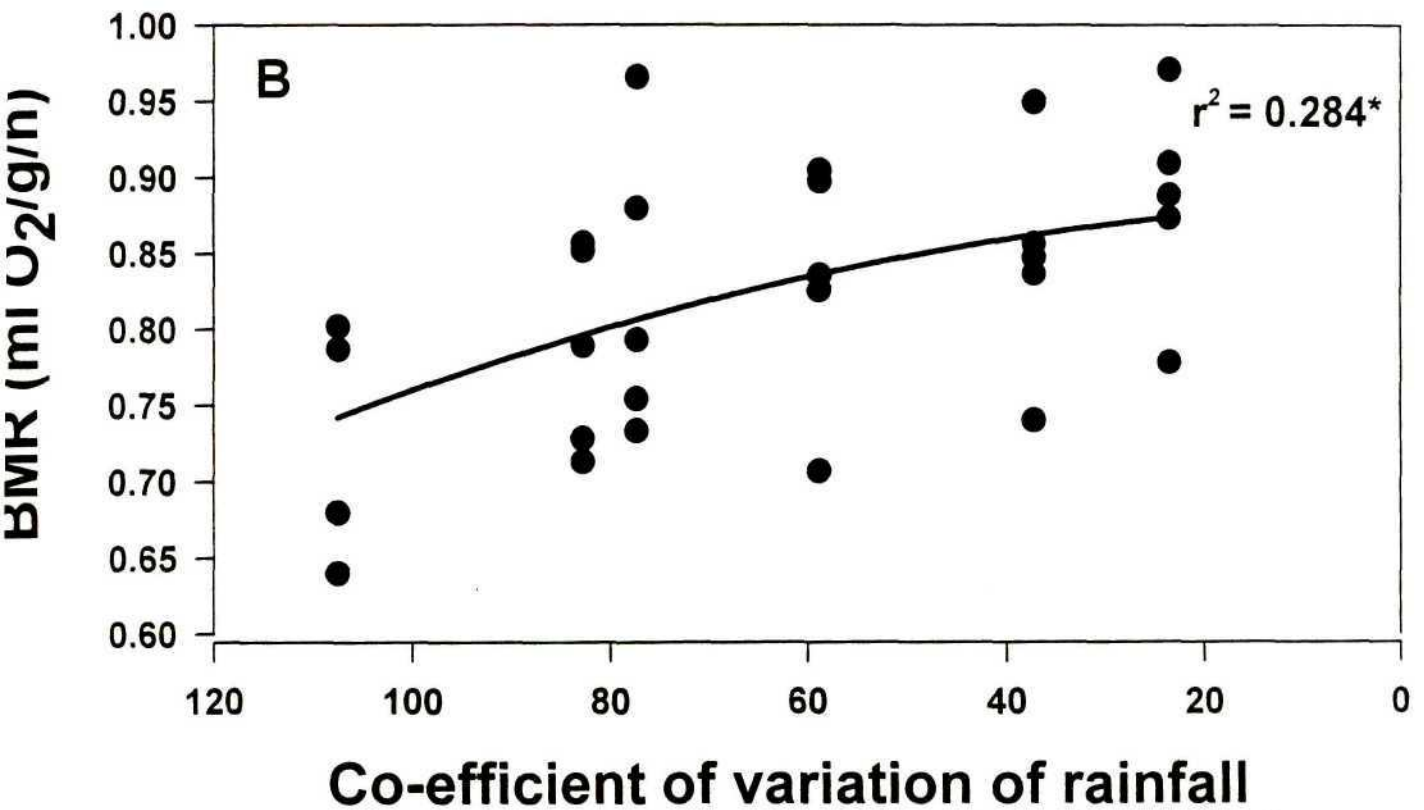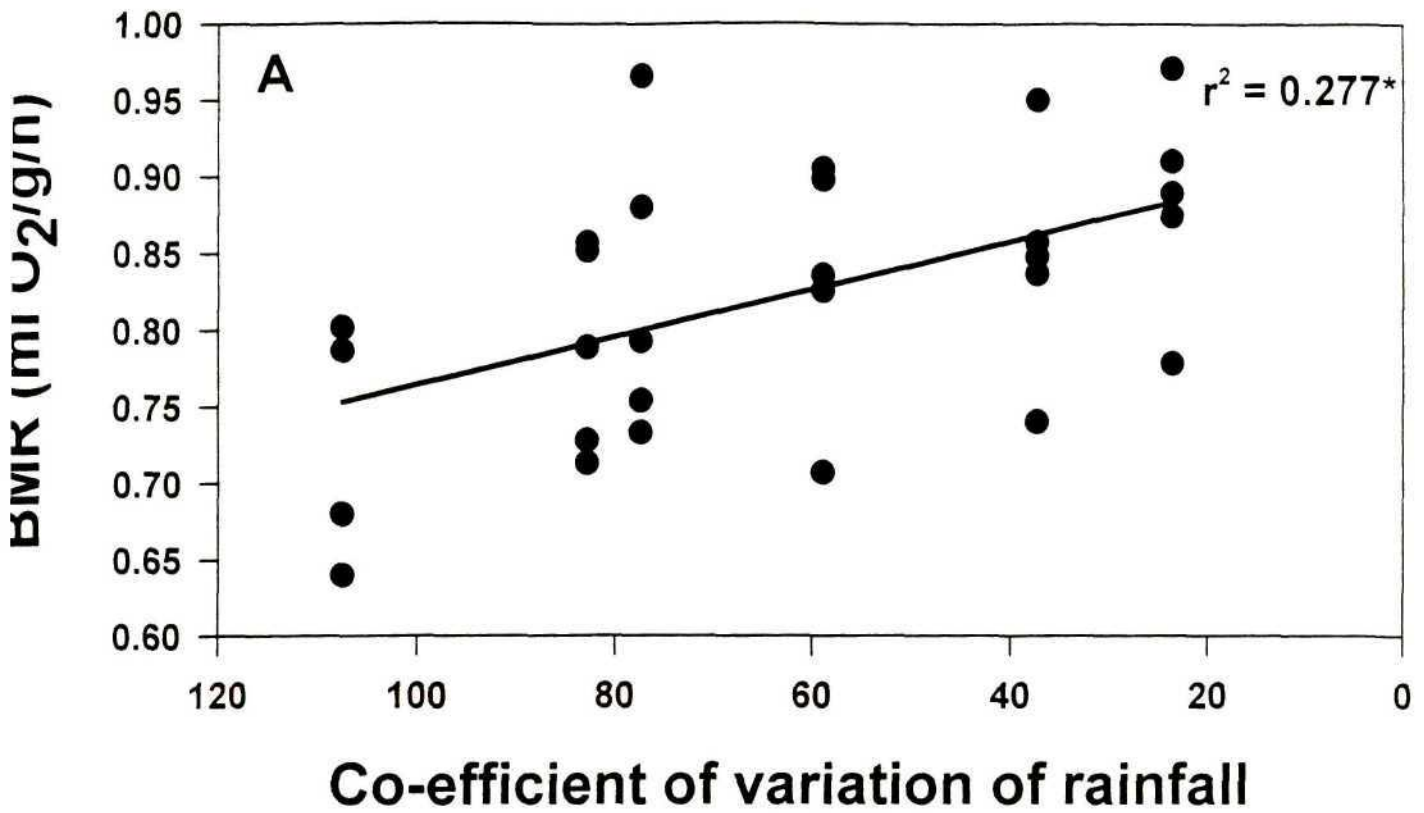
Fig. 16: A) First and b) second order quadratic regressions fitted to basal metabolic rate (BMR) of thirty rodents (*Rhabdomys pumilio*) from six geographical areas in southern Africa, as a function of the co-efficient of variation of mean annual rainfall of the area. * denotes statistical significance (p < 0.05).
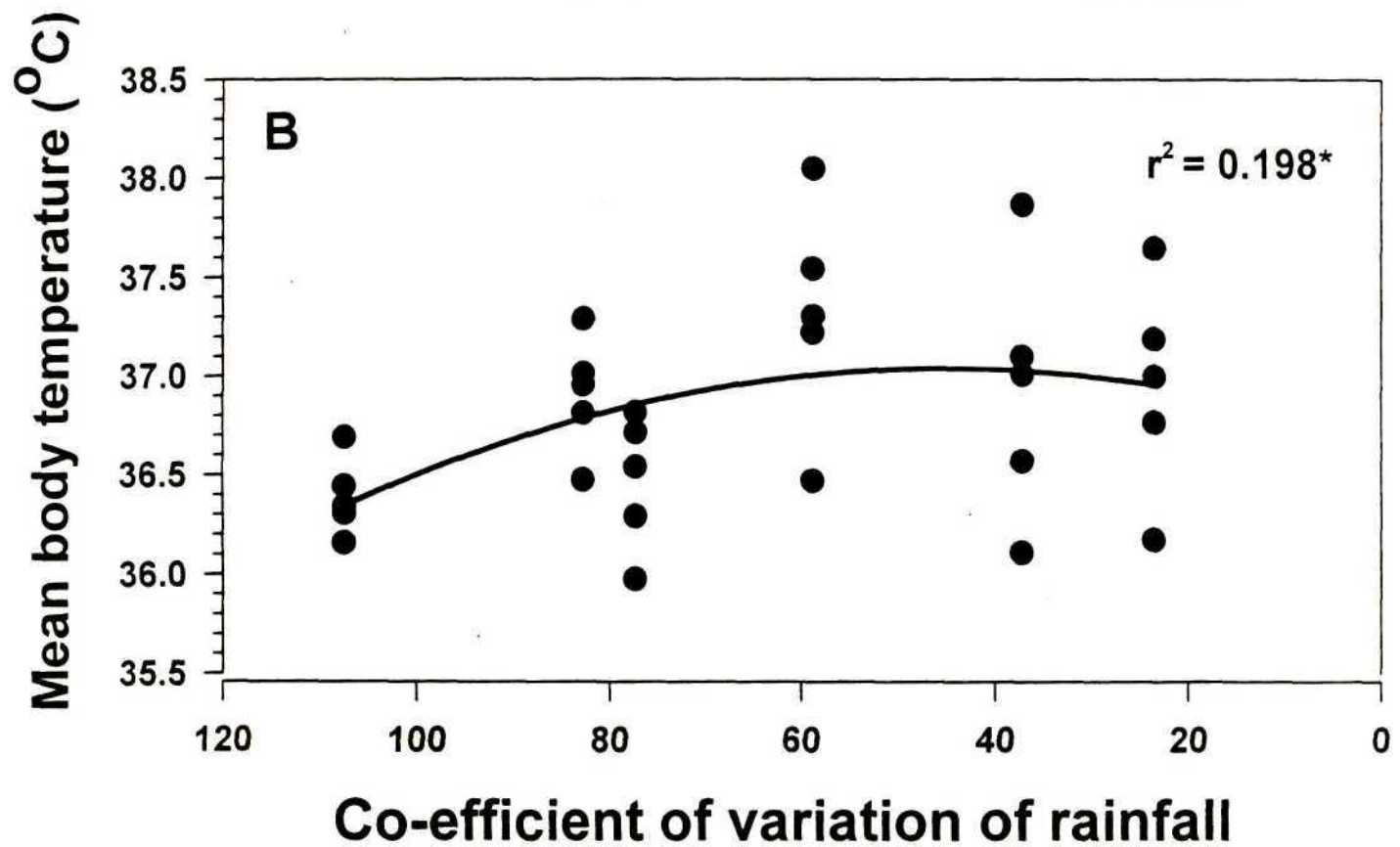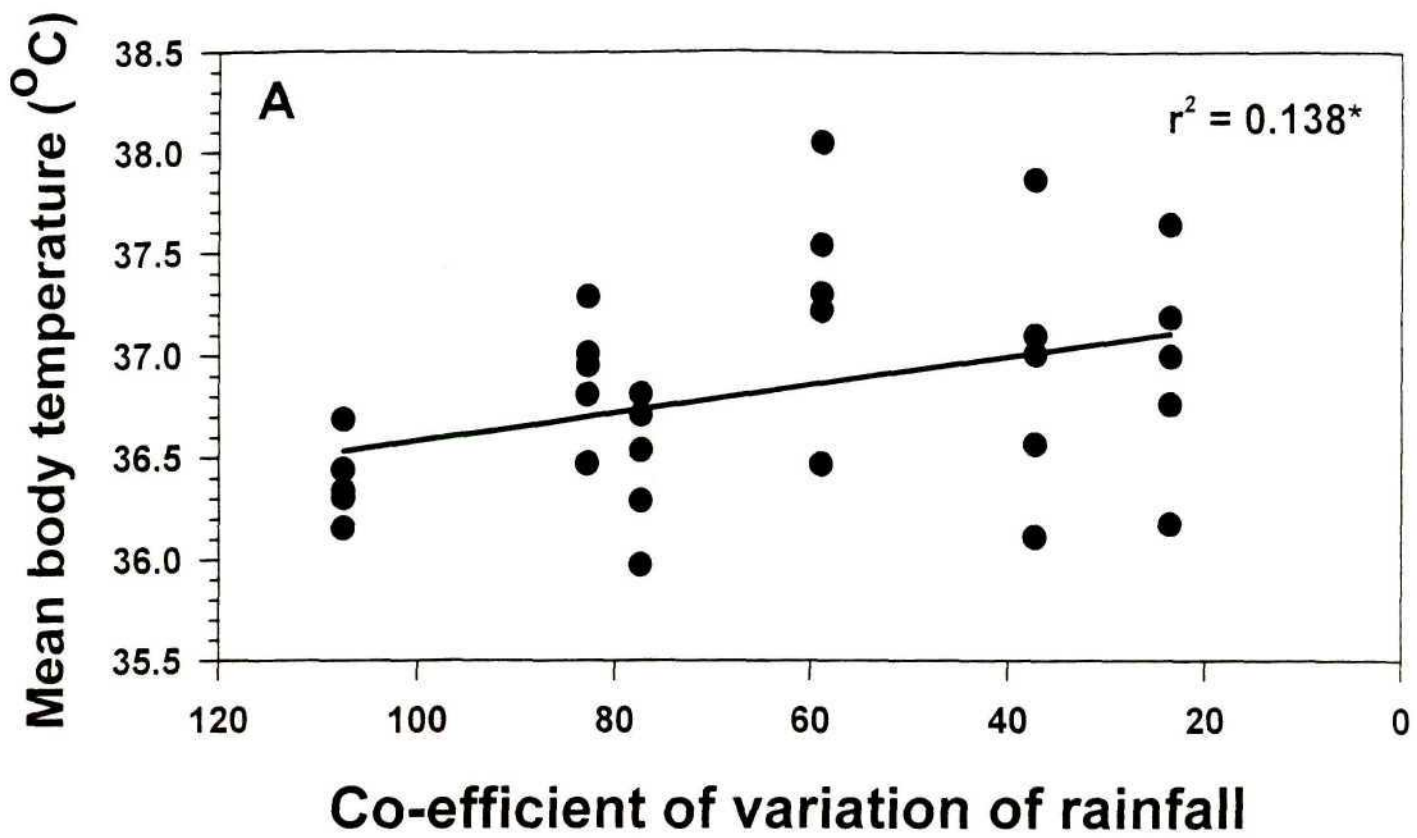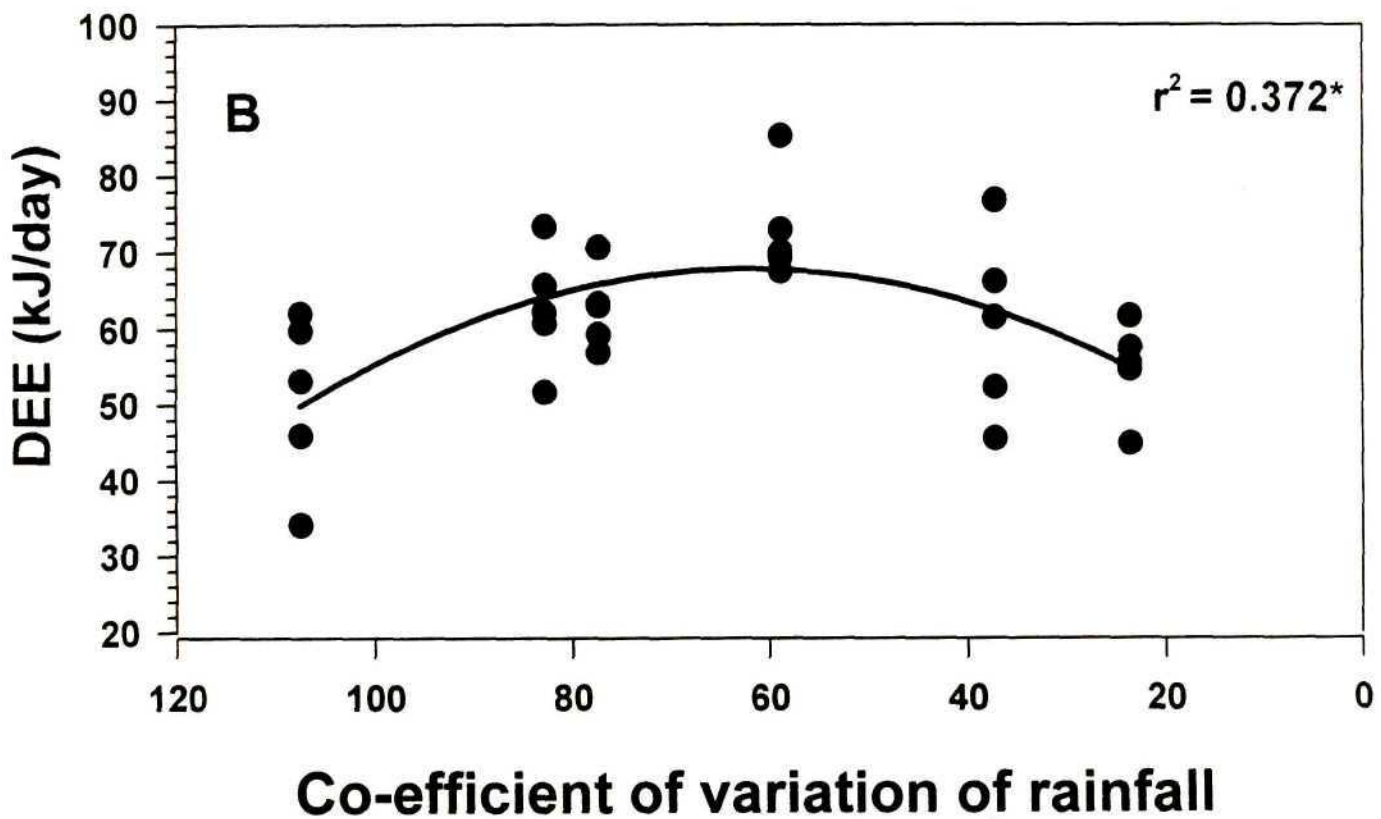
Fig. 17: A) First and b) second order quadratic regressions fitted to mean body temperature of thirty rodents (*Rhabdomys pumilio*) from six geographical areas in southern Africa, as a function of the co-efficient of variation of mean annual rainfall of the area. Ambient temperature was 30°C. * denotes statistical significance (p < 0.05).
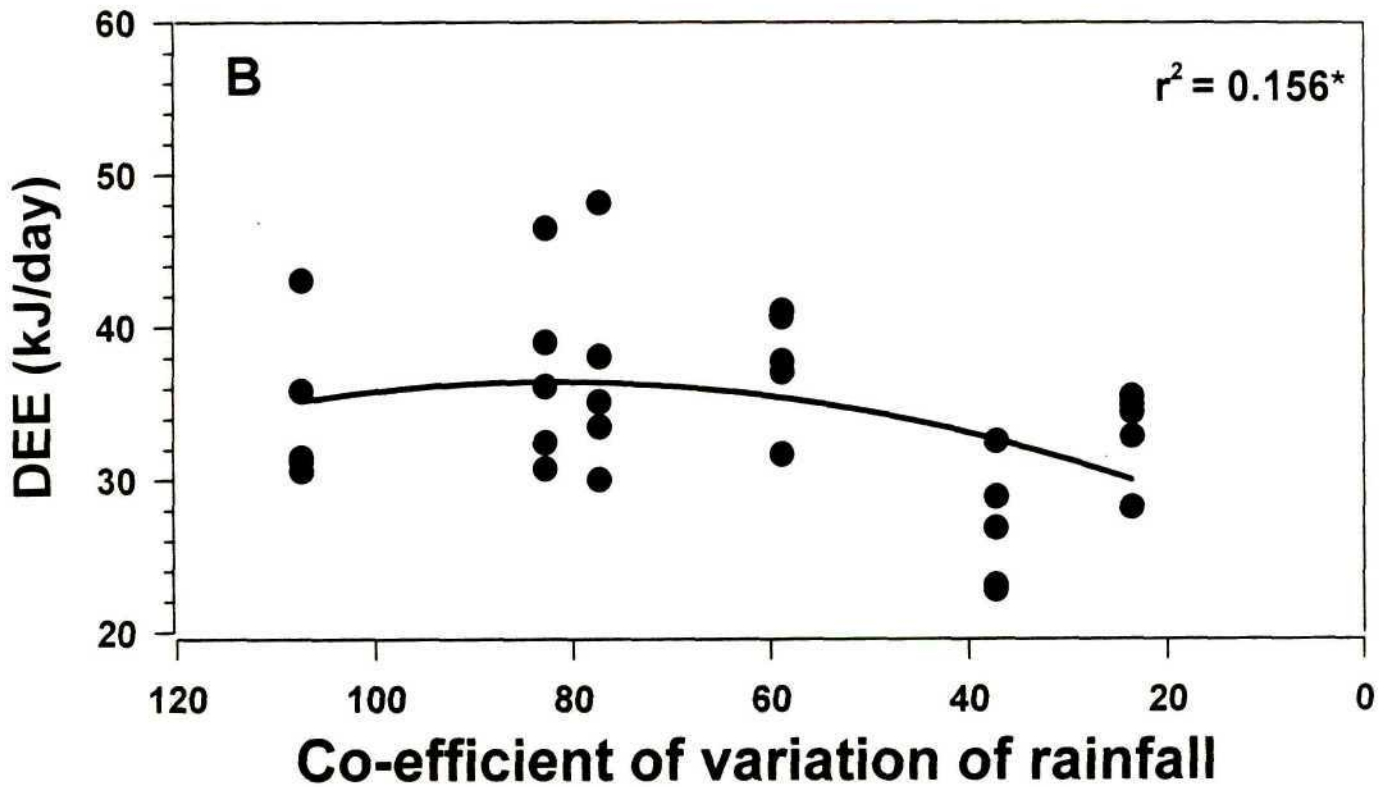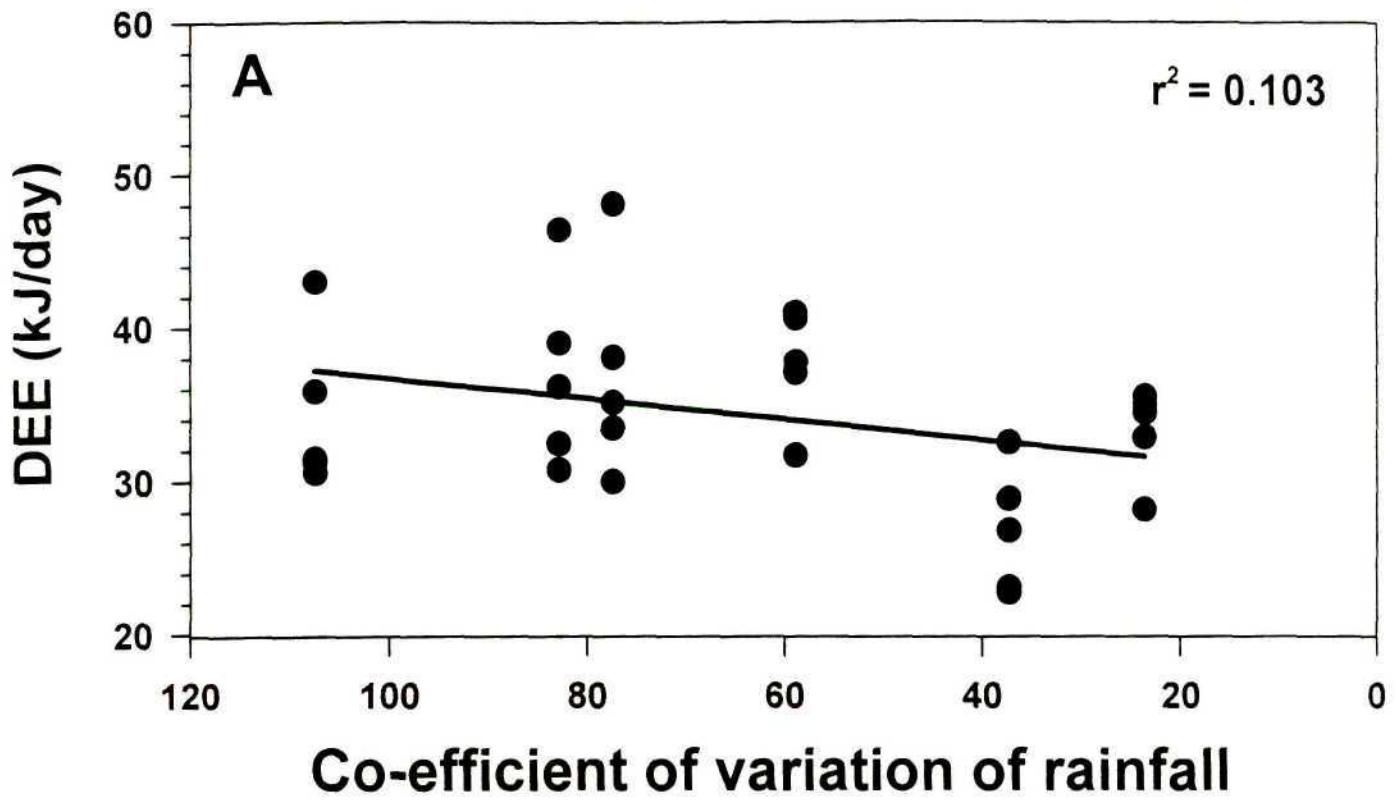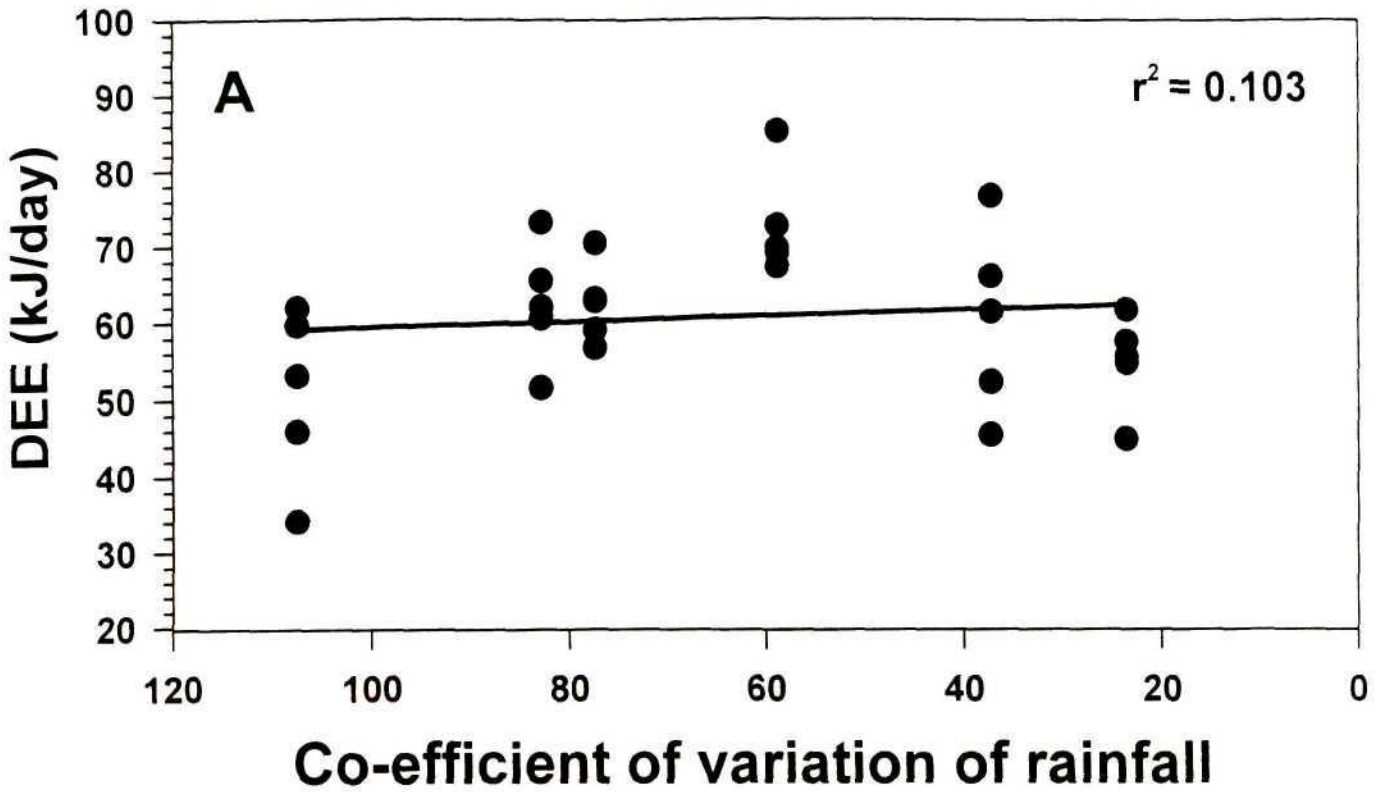
Fig. 18: A) First and b) second order quadratic regressions fitted to daily energy expenditure (DEE) of thirty rodents (*Rhabdomys pumilio*) from six geographical areas in southern Africa, as a function of the co-efficient of variation of mean annual rainfall of the area. Ambient temperature was 30°C. * denotes statistical significance ($p < 0.05$).
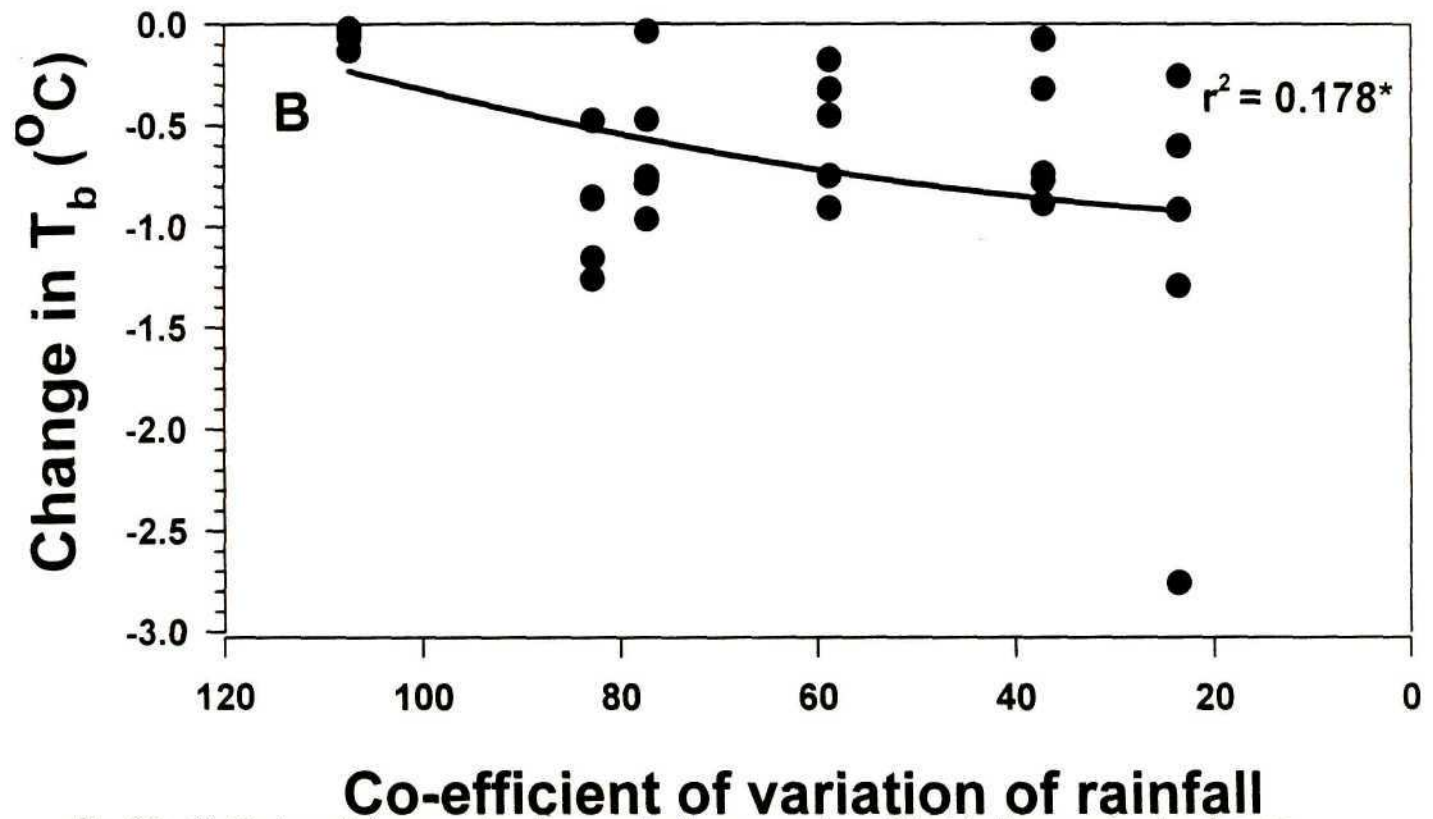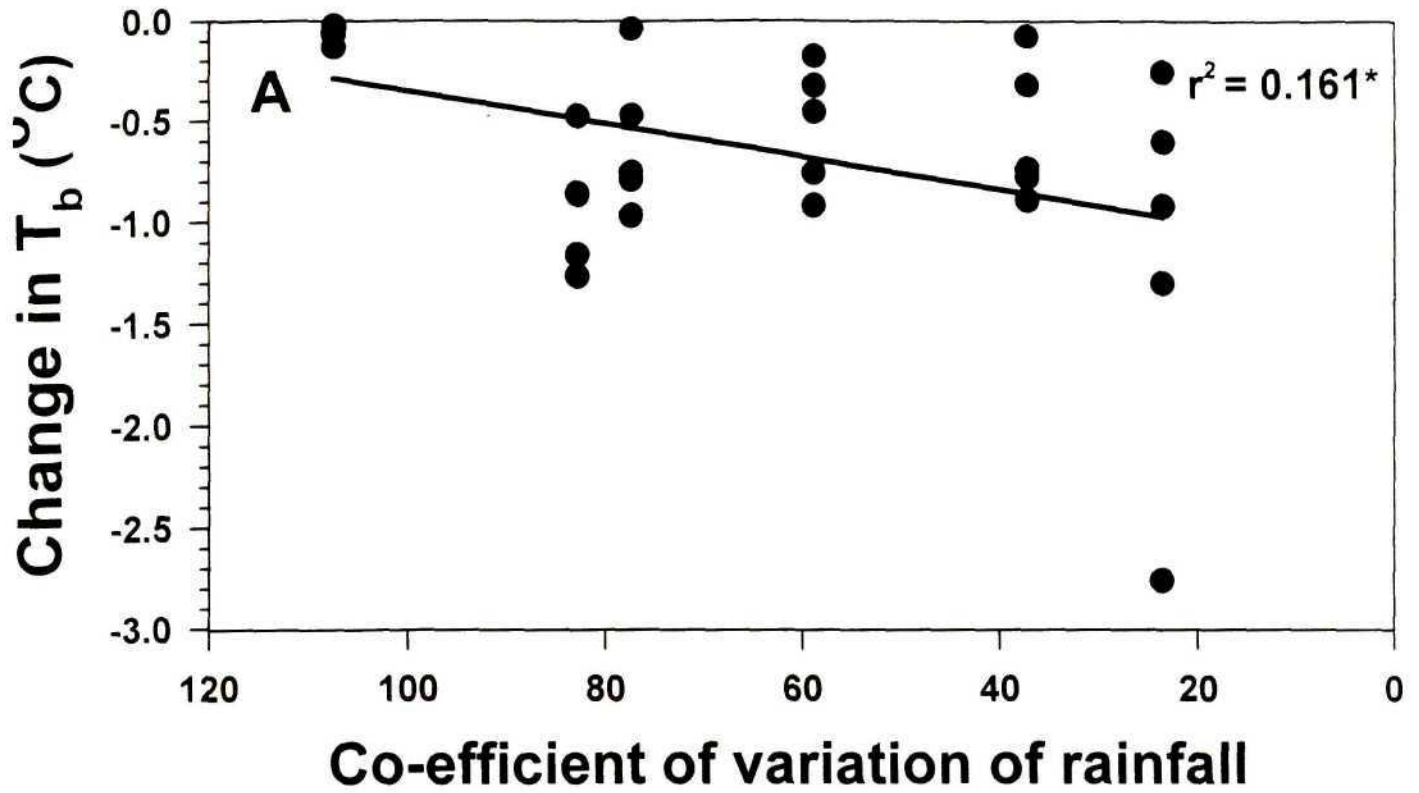
Fig. 19: A) First and b) second order quadratic regressions fitted to daily energy expenditure (DEE) of thirty rodents (*Rhabdomys pumilio*) from six geographical areas in southern Africa, as a function of the co-efficient of variation of mean annual rainfall of the area. Ambient temperature was 20°C. * denotes statistical significance (p < 0.05).

Fig. 20: A) First and b) second order quadratic regressions fitted to the proximate change in average body temperature from $T_a = 30°C$ to $T_a = 20°C$. Results are plotted for thirty rodents (*Rhabdomys pumilio*) from six geographical areas in southern Africa, as a function of the co-efficient of variation of mean annual rainfall of the area. * denotes statistical significance ($p < 0.05$).
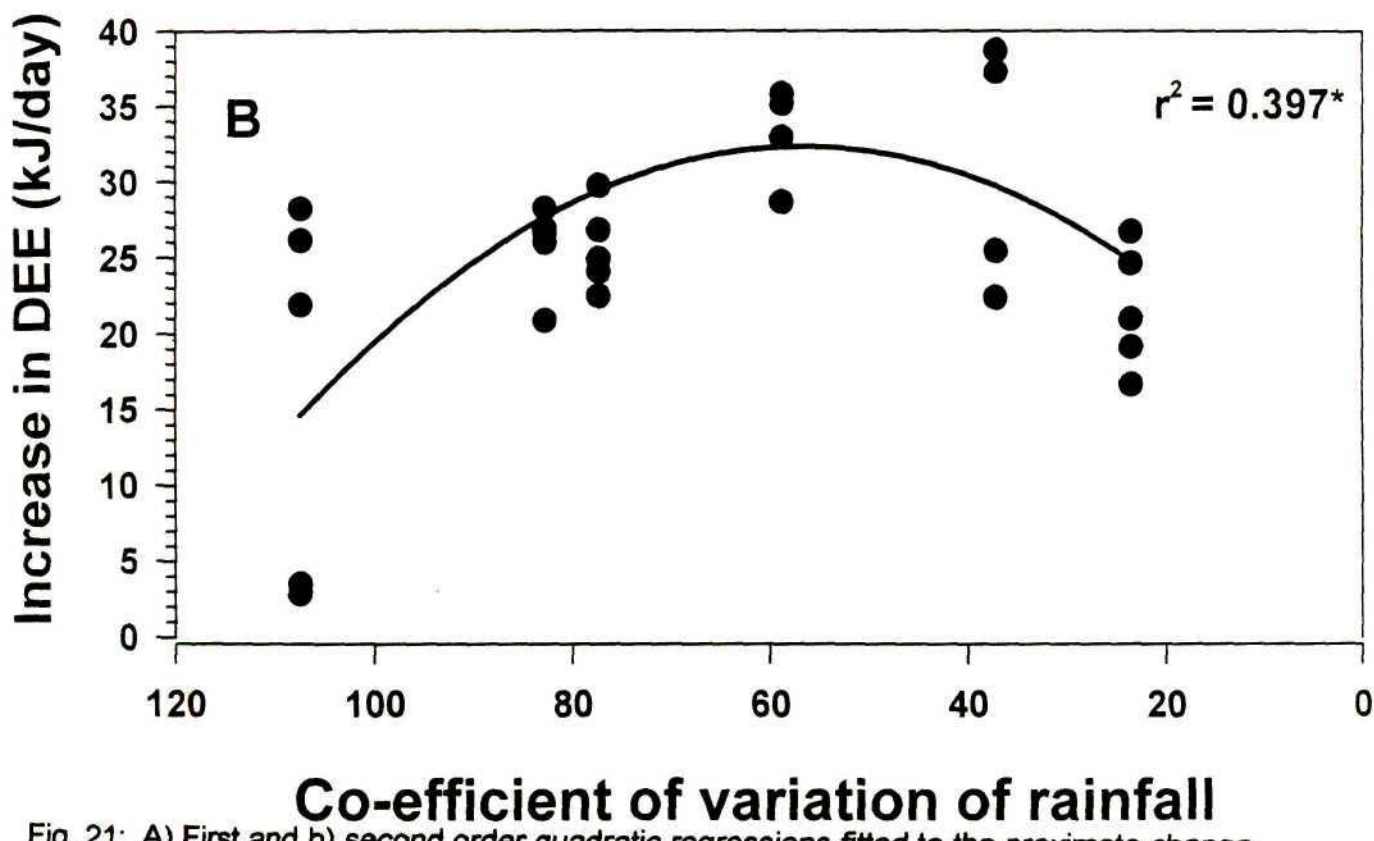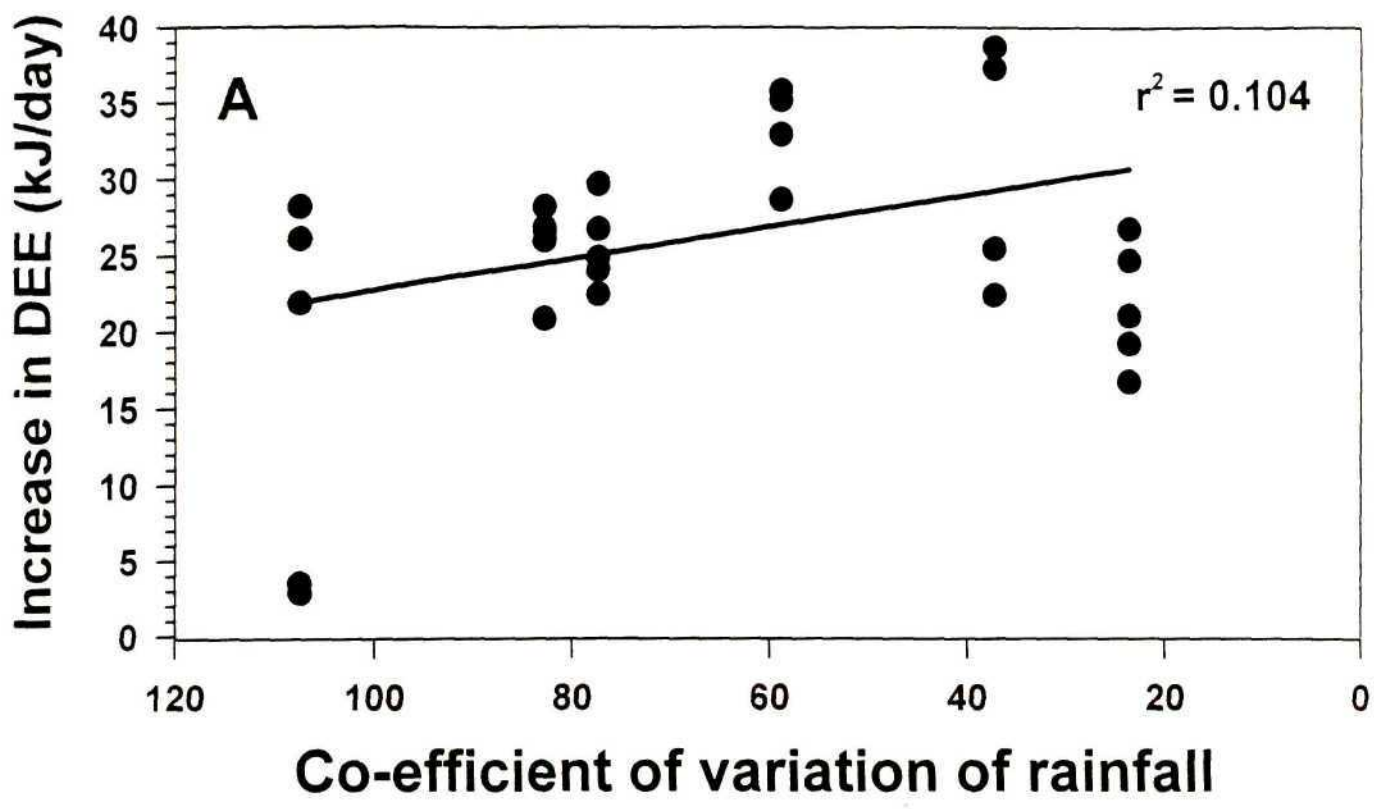
Fig. 21: A) First and b) second order quadratic regressions fitted to the proximate change in energy expenditure from $T_a = 30°C$ to $T_a = 20°C$. Results are plotted for thirty rodents (*Rhabdomys pumilio*) from six geographical areas in southern Africa, as a function of the co-efficient of variation of mean annual rainfall of the area. * denotes statistical significance ($p < 0.05$).