Aspects of the thermal ecology of the group-living lizard, *Cordylus cataphractus*: A spatial and temporal analysis

by
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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained herein is my own, original work, and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

March 2011

Abstract

Thermal ecology is a central theme in reptilian biology because of the thermodynamic rate dependence of virtually all biological processes in these ectothermic animals. Thermoregulation includes active processes (with associated energetic costs related to altered behaviour and physiology) functioning to maintain body temperatures within a preferred temperature range, so that the majority of physiological functions occurs optimally, despite natural variation in the animal's thermal habitat. The recent development of quantitative thermal indices now allows researchers to describe the thermal habitat and thermoregulatory functioning of an ectotherm within its environment from a cost-benefit perspective. The use of such quantitative biophysical approaches to reptile thermal ecology studies is however limited in the African context. *Cordylus cataphractus* is one of the best studied cordylids, and exhibits various characteristics atypical for the family, such as permanent group-living, seasonally lowered surface activity, a low resting metabolic rate and large fat bodies. These characteristics are generally thought to be associated with group-living in a semi-arid habitat, yet, the possible links to thermal ecology remains unexplored.

The objectives of the current study was: firstly, to characterize the preferred temperature range (T_p) of *C. cataphractus* through the use of ecologically realistic laboratory thermal gradients; secondly, to explore seasonal and geographical variation in thermal preference, by comparing T_p among individuals captured from a coastal and inland population and during different seasons (autumn and spring); thirdly, to describe the thermal habitat of a *C. cataphractus* population during summer, autumn, winter and spring and to then relate these findings to the seasonal activity patterns reported in literature for the species; fourthly, to describe the seasonal patterns of thermoregulation (during summer, autumn, winter and spring) in a *C. cataphractus* population through quantitative thermoregulatory indices; fifthly, to assess geographic variation in the thermal habitat and

associated patterns of thermoregulation in *C. cataphractus* among a coastal population (western range limit) and an inland population (eastern range limit). The thermal habitat of *C. cataphractus* was described by measuring operative environmental temperatures (T_e) with hollow copper lizard models placed around rocks according to the natural surface movement patterns of the species. Variation in thermal habitat quality was subsequently calculated (d_e = |T_e − T_p|) and averaged. Field body temperatures (T_b) of lizards were measured with dorsally attached miniature temperature loggers. Thermoregulatory indices were calculated from T_e, T_b and T_p, describing: thermoregulatory accuracy, the effectiveness of thermoregulation and thermal exploitation for each population (coastal and inland) for the respective sampling periods.

The preferred body temperature range of *C. cataphractus* is the lowest recorded among cordylids to date (mean T_p = 29.8^{o}C) and was conserved among different populations and within these populations among seasons, despite the fact that environmental temperatures are known to vary geographically and seasonally.

Thermal habitat quality varied significantly at micro spatial scale around rocks in the coastal population. Since *C. cataphractus* males are territorial, competition for thermal habitat quality around rocks may therefore occur. Such effects will be a function of the time of year since the variability in thermal habitat quality among rock aspects (around rocks) varied seasonally.

Thermal habitat quality of crevices varied among seasons and was typically higher in the open, outside rock crevices, during the cooler winter and spring periods, whereas in summer and autumn the crevice environments were more favourable. Thermal habitat quality was high in crevices during autumn, suggesting that the observed repressed surface activity of *C. cataphractus* described for the time is not necessarily, as previously thought, only due to food constraints. Moreover, in contrast to earlier reports, the current results (T_b versus T_e) indicate that individuals emerged from crevices in summer.

The geographical assessment indicated that lizards from the coastal population, with generally larger groups, thermoregulated more successfully than those from the inland

population. The higher thermoregulatory success in the coastal population occurred in spite of the fact that thermal habitat quality was significantly lower at the coastal locality. The higher thermoregulatory success in the coastal population was likely due to reduced predation risk associated with increased group-size. The seasonal trends in thermoregulation at the coastal and inland population corresponded to the patterns predicted by the cost-benefit model of thermoregulation, accuracy of thermoregulation and the effectiveness of thermal exploitation being higher during the thermally more favourable autumn.

Uittreksel

Termiese ekologie is 'n sentrale tema in reptiel-biologie as gevolg van die termodinamies tempo-afhanklikheid van feitlik alle biologiese prosesse in hierdie ektotermiese diere. Termoregulering sluit aktiewe prosesse (wat lei tot energie-koste in terme van gedrag en fisiologie) in om liggaamstemperature binne 'n vasgestelde voorkeurtemperatuur-reeks te handhaaf sodat fisiologiese prosesse optimaal kan geskied te midde van natuurlike variasie in die dier se termiese omgewing. Die onlangse ontwikkeling van kwantitatiewe funksionele termiese indekse stel navorsers nou in staat om die werklike termiese omgewing en die funksionering van die ektoterm binne sy omgewing te beskryf en uit 'n koste (energie)-voordeel oogpunt te verstaan. Die gebruik van hierdie biofisiese koste-voordeel benadering in reptiel termoreguleringstudies is egter beperk in die Afrika-konteks. *Cordylus cataphractus* is een van die bes bestudeerde lede van familie Cordylidae, en vertoon verskeie eienskappe ongewoon vir hierdie groep akkedisse, soos groeplewendheid, beperkte seisoenale aktiwiteit buite hul skeure, 'n relatiewe lae rustende metaboliese tempo en relatiewe groot vetliggame. Hierdie unieke eienskappe is al deur navorsers gekoppel aan die groeplewe lewens-strategie. Die potensiële koppeling van die termiese ekologie en die spesifieke lewens-strategie van *C. cataphractus* benodig verdere studie. Die doelwitte van hierdie studie was eerstens: om die voorkeurtemperatuur-reeks (T_p) van *C. cataphractus* te bepaal deur van ekologies-realistiese termiese gradiënte in die laboratorium gebruik te maak; tweedens: om geografiese en seisoenale variasie in T_p te ondersoek deur individue te gebruik wat uit binnelandse en kus-populasies, tydens verskillende seisoene, herfs en lente versamel is; derdens: om die termiese omgewing, meer spesifiek die variasie in termiese kwaliteit, binne die habitat van 'n *C. cataphractus* populasie in verskillende seisoene, somer, herfs, winter en lente, te moduleer en met die gedokumenteerde aktiwiteitspatrone in verband te bring; vierdens: om die seisoenale temoreguleringspatrone (tydens somer, herfs, winter en lente) van 'n *C. cataphractus* populasie te beskryf; vyfdens: om geografiese variasie in die termiese habitat en geassosieerde termoreguleringspatrone tussen 'n kus-populasie (westelike

verspreidingsgrens) en 'n binneland-populasie (oostelike verspreidingsgrens) te bestudeer. Die kwaliteit van die termiese habitat van *C. cataphractus* is bepaal deur hol koper-modelle van akkedisse (operatiewe temperatuur modelle (T_e)) te plaas rondom rotse in ooreenstemming met die natuurlike bewegingspatrone van die akkedisse. Die termiese kwaliteit is gevolglik afgelei ($d_e = |T_e - T_p|$) en gemiddeldes bereken. Die liggaamstemperature (T_b) van vrylopende akkedisse in die veld is met dorsaal-gemonteerde miniatuur temperatuur "data-loggers" gemeet. Termiese indekse (deur T_e, T_b en T_p te gebruik) is bereken om die akkuraatheid en effektiwiteit van termoregulering, sowel as termiese benutting van die omgewing vir beide populasies (kus en binneland) tydens verskillende seisoene te beraam.

Die voorkeurtemperatuur-reeks van *C. cataphractus* is die laagste gedokumenteerde temperature vir enige lid van die familie Cordylidae tot op hede bestudeer (gemiddeld van T_p = 29.8^{o}C), en het ten spyte van die feit dat omgewingstemperature wissel op geografiese en seisoenale vlakke, min gevarieer tussen die twee populasies asook tydens verskillende seisoene binne die populasies.

Die termiese kwaliteit het beduidend gevarieer tussen seisoene en binne die mikro-ruimtelike omgewing rondom rotse in die kus-populasie. Aangesien *C. cataphractus* mannetjies territoriaal is, word die aanname gemaak dat kompetisie vir 'n ruimtelike posisie ook 'n termiese koste mag hê aangesien daar beduidende variasie in d_e om die rotse was. Variasie in termiese kwaliteit rondom rotse was verder ook 'n funksie van die tyd van die jaar (seisoene).

Die termiese kwaliteit van skeure het gevarieer tussen seisoene, en termiese kondisies/toestande was oor die algemeen meer gunstig buite die rots-skeure tydens die koeler winter en lente tydperke, terwyl skeure termies meer gunstig was in die somer en herfs maande. Termiese habitat kwaliteit van skeure was besonders hoog gedurende die herfs, en die voorspelling is dus dat die verlaagde oppervlak-aktiwiteit wat gedurende hierdie tyd van die jaar vir *C. cataphractus* gedokumenteer is nie noodwendig 'n funksie van beperkte voedselbeskikbaarheid is nie. Teenstrydig met gepubliseerde aktiwiteitsrekords dui

die resultate (T_b teenoor T_e) verder daarop dat individue wel uit skeure kom tydens die warm somer seisoen.

Die geografiese ondersoek het gewys dat akkedisse van die kus-populasie (wat gewoonlik uit groter groepe bestaan), meer akkuraat getermoreguleer het as akkedisse van die binneland-populasie. Die hoër akkuraatheid van termoregulering in die kus-populasie is bewerkstellig ten spyte van die feit dat die termiese kwaliteit beduidend laer was as die van die binneland-populasie. Die hoër termoreguleringsakkuraatheid in die kus-populasie kan waarskynlik toegeskryf word aan 'n laer predasie-risiko geassosieer met groter groepe. Die seisoenale variasie-patroon van termoregulering kan verklaar word deur die koste-voordeel model van termoregulering, waarvolgens die akkuraatheid van termoregulering sowel as termiese benutting hoër is tydens periodes van hoë termiese kwaliteit (i.e. herfs).

Dedication

I dedicate this thesis to the God of Heaven, the Almighty, my Father...in appreciation of His

endless love and grace towards me.

Acknowledgements

I would like to thank the following people and organizations whose contributions made the study possible:

Metrics and indices of thermal ecology

Metric or Symbol	Description
T_p	The preferred temperature range (T_p), describes the range of body temperatures at which physiological functioning is optimized, therefore representing the target of thermoregulation. These "ideal" body temperatures are measured in a laboratory thermal gradient (theoretically) in the absence of ecological costs.
T_e	Environmental operative temperatures (T_e) describe the available equilibrium body temperatures which an animal will experience in a specific habitat in the absence of thermoregulation (measured with physical copper models that represent lizards in size, shape and skin coloration) (Bakken 1992).
T_b	Field body temperatures are measured on a representative sample of individuals with cloacal temperature probes, temperature sensitive telemetry or miniature temperature loggers implanted or attached externally to animals.
d_e	Thermal habitat quality expresses the degree to which operative environmental temperatures (T_e) match the target preferred temperature range (T_p), and is calculated from the absolute deviation of T_e from T_p (d_e = [T_e − upper limit of T_p], if $T_e > T_p$: d_e = [lower limit of $T_p − T_e$], if $T_e = T_p$, d_e = 0). The degree to which T_e deviates from T_p describes thermal suitability from the organism's perspective and hence thermal quality (Hertz *et al.* 1993).
d_b	Accuracy of thermoregulation expresses the degree to which T_bs attained in the field matched the target preferred temperature range (T_p) and is calculated from the absolute deviation of T_b from T_p (d_b = [T_b − upper limit of T_p], if $T_b > T_p$: d_b = [lower limit of $T_p − T_b$], if $T_b = T_p$, d_b = 0). A high d_b-value therefore expresses low accuracy (Hertz *et al.* 1993).
$d_e − d_b$	The effectiveness of thermoregulation considers accuracy of thermoregulation as a function of the available thermal quality, describing the departure from thermoconformity. The $d_e − d_b$ index is simply calculated from the difference between d_e and d_b. Values approaching one indicate active thermoregulation, whereas those approaching zero indicate thermoconformity (Blouin-Demers and Weatherhead 2001).
E_x	Thermal exploitation describes the extent to which animals exploit the favourable opportunities for thermoregulation available to them, calculated as: (time in which $T_b = T_p$) / (time in which any T_e observed in the habitat = T_p) x 100 % (Christian and Weavers 1996).

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Chapter 1

General introduction

1.1 Reptile thermal ecology and the quantitative assessment thereof

1.1.1 Reptile thermoregulation

Animal body temperature affects all levels of physiology, from enzyme reactions to processes such as digestion, locomotion and growth (Huey 1982; Stevenson *et al.* 1985; Seebacher and Franklin 2005). Mammals and birds (i.e. endotherms) may be viewed as extreme thermal specialists, maintaining body temperatures within a narrow set-point range, despite variation in environmental temperatures (Hafez 1964; Bligh 1998; Ivanov 2005). Endotherm T_b-control is administered through a suite of physiological, behavioural and morphological mechanisms (e.g. metabolic heat production, insulation, behaviour, evaporative cooling, panting and cardiovascular mechanisms) (reviewed by Hafez 1964 and Bligh 1998) which may be highly taxing to the time- and energy budgets of animals (Bennett and Ruben 1979; Pough 1980). In contrast to endotherms, reptiles have a more relaxed "set-point" (target) temperature range (especially when external heat sources are limited) known as the preferred temperature range (T_p), at which the majority of physiological functions occur optimally (Licht *et al.* 1966; Hertz *et al.* 1993; Angilletta *et al.* 1999). The preferred temperature range can be estimated in an artificial laboratory thermal gradient where both physical and biotic constraints are theoretically minimized (Licht *et al.* 1966; Stevenson *et al.* 1985; Angilletta *et al.* 1999; Clusella-Trullas *et al.* 2007).

Although physiological control may contribute to thermoregulation (reviewed in Bartholomew 1982), reptiles rely primarily on behavioural mechanisms (i.e. shuttling, orientation, postural adjustments, microsite selection) to attain external heat and maintain T_b near to the preferred range (Huey 1982; Stevenson 1985; Bauwens *et al.* 1996). Thermal (energy) gain or loss therefore occurs predominantly through the exploitation of environmental heat loads (Figure 1.1) (Pough 1980; Angilletta 2009), an approach (to T_b-

control) that may have significant effects on daily energy expenditure (Bennett and Nagy 1977; Pough 1980). For example, consider the classic study of Bennet and Nagy (1977) which demonstrates that the lizard, *Sceloporus occidentalis* maintains a daily metabolic expenditure 96 % to 97 % lower than that expected for a mammal or bird of equal size (Bennett and Nagy 1977). The implication of lower metabolic rates however is lower heat production and therefore high dependence on external heat sources during cooler periods.
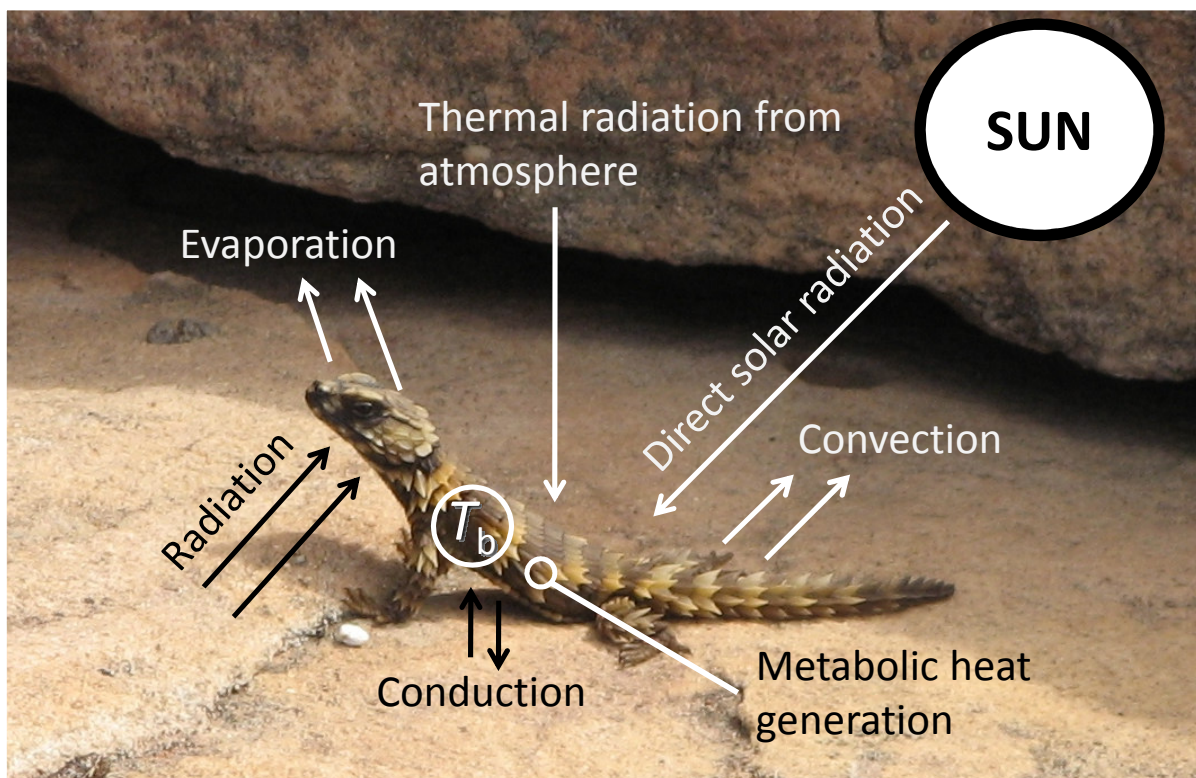
Figure 1.1. Heat transfer pathways experienced by field-active lizards that may affect field body temperatures (T_b) (adopted from Bartholomew (1986)).

Two main approaches to body temperature control have been identified in reptiles namely: thermal generalists (i.e. eurytherms/thermoconformers) and thermal specialists (i.e. stenotherms/strict thermoregulators) (Huey 1982; Gilchrist 1995; Herczeg *et al.* 2008). In theory, thermal generalists have wide performance breadths and are therefore able to be active at a wide range of body temperatures, whereas, thermal specialists typically have

narrow performance breadths, and maintain T_b within a narrow range during activity (Bowker and Johnson 1980; Huey 1982; Bowker 1984; Herczeg *et al.* 2008).

The thermoconformer-thermoregulator systems are however a continuum (not set in stone) and in reality, the extent of thermoregulation varies greatly within and among reptile taxa, and even within species at seasonal scales (Huey 1974; Hertz *et al.* 1993; Schauble and Grigg 1998). For example, *Anolis cristatellu*s may change from being strict thermoregulator in one season to thermoconformer in the next (Huey 1974; Huey and Webster 1976; Hertz *et al.* 1993). The consideration is that the relative position along the thermoregulate–thermoconform continuum (at a specific point in time) is a function of the unique cost-to-benefit ratios present within a particular species (Huey and Slatkin 1976).

1.1.2 A null model is needed

For decades researchers assessed the extent of thermoregulatory behaviour simply by comparing field body temperatures with air temperature (T_{air}) (Huey 1982; Hertz *et al.* 1993; Angilletta 2009). Heath (1964) brought a major advancement to the field of thermal ecology when he, with the use of beer cans filled with water, demonstrated that air temperatures may be a misrepresentation of thermal opportunities to animals, since some of the cans seemingly "thermoregulated" reaching temperatures exceeding T_{air} by up to 8°C. The logic introduced by Heath (1964) eventually led to the birth of operative temperature models, physical models that match live animals in size, shape and radiative properties, thus integrating all the factors that influence heat exchange between the animal and its environment (Figure 1.1) (Bakken and Gates 1975; Bakken 1992; Diaz and Cabezas-Diaz 2004; Dzialowski 2005). Environmental operative temperatures (T_e) therefore describe the T_bs (integrating all biophysical effects) an animal will experience by simply being present in a specific habitat (potential T_bs) and may therefore function as a null model for thermoregulation from which the amount of thermoregulation performed (costs) can be quantified (Hertz *et al.* 1993; Bauwens *et al.* 1996; Diaz 1997; Diaz and Cabezas-Diaz 2004).

1.1.3 The Hertz *et al.* (1993) protocol

Hertz *et al.* (1993) devised a protocol to quantitatively describe the (field) thermal ecology of small reptiles in virtually any context, among other outcomes, allowing researchers to estimate the position of a reptile species or population along the thermoregulate-thermoconform continuum. The protocol is based on three metrics namely: (1) the theoretic "target" preferred temperature range (T_p); (2) the available body temperatures describing zero thermoregulation (T_e); (3) actual field body temperatures (T_b) recorded through radio telemetry, cloacal probes or small temperature data loggers attached to the body surface. Hertz *et al.* (1993) applied these aforementioned metrics collectively to describe reptile thermal ecology as follows:

Firstly, the absolute deviation of T_e from T_p describes thermal habitat quality (d_e) (reflecting the degree of active thermoregulation needed to function within T_p). A high d_e therefore denotes low quality from the organism's perspective.

Secondly, the absolute deviation of T_b from T_p describes the accuracy of thermoregulation (d_b) (reflecting the success with which an organism is able to maintain T_b near to or within T_p). A high d_b therefore denotes low thermoregulatory accuracy.

Thirdly, accuracy of thermoregulation (d_b) as a proportion of thermal habitat quality (d_e) describes the effectiveness of thermoregulation (E); therefore indicating to what extent the organism's ability to maintain T_b near T_p exceeds the opportunity provided by the thermal habitat to maintain T_b near T_p (i.e. the extent of thermoregulation performed). Effectiveness (E) ranges between zero and one, values approaching one indicates active thermoregulation, whereas those approaching zero indicate thermo conformity.

The Hertz *et al.* (1993) protocol transitioned the field of thermal ecology by providing a standard framework for inter-species, inter-population comparisons. The protocol has been applied to a variety of reptile groups including: lizards (Clusella-Trullas *et al.* 2009; Harlow *et al.* 2010); snakes (Row and Blouin-Demers 2006; Lelievre *et al.* 2010); turtles (Edwards and

Blouin-Demers 2007; Bulte and Blouin-Demers 2010) and amphisbaenians (Lopez *et al.* 1998; Lopez *et al.* 2002).

1.1.4 The Hertz *et al.* (1993) protocol and improvements

Although widely accepted, critique has been raised against the Hertz *et al.* (1993) protocol (Christian and Weavers 1996; Currin and Alexander 1999; Blouin-Demers and Weatherhead 2001). Specifically, the application of the effectiveness (E) index has been questioned for three reasons: E is undefined when thermal habitat quality is perfect ($d_e = 0$), E cannot be interpreted without taking the respective magnitudes of d_e and d_b into account (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Nadeau 2005), and E is a ratio, making it sensitive to extreme values (Christian and Weavers 1996) which might therefore result in superious representations of reptile thermoregulation (Blouin-Demers and Nadeau 2005).

As a replacement for E, Blouin-Demers and Weatherhead (2001) proposed the $d_e - d_b$ index for effectiveness of thermoregulation. The magnitude of the difference between d_e and d_b quantifies the degree of departure from thermoconformity ($d_e - d_b = 0$: perfect thermoconformity), and the output therefore corresponds to the Hertz *et al.* (1993) effectiveness index (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Weatherhead 2002; Blouin-Demers and Nadeau 2005).

Christian and Weavers (1996) described the thermal exploitation index (E_x) describing the degree to which a reptile exploits the available opportunities for precise thermoregulation. One of the advantages of the E_x index is the fact that it expresses the animal's thermoregulatory responses independent of the thermal habitat quality. Thermal exploitation E_x is calculated by dividing the time that T_bs are within T_p, by the time that any T_e present in the habitat is within T_p (i.e. T_e would allow T_p to be achieved) therefore describing the time-fraction (%) during which T_b equals T_p when permissive in a habitat.

By using a combination of thermal quality (d_e), accuracy of thermoregulation (d_b) (Hertz *et al.* 1993), effectiveness of thermoregulation ($d_e - d_b$) (Blouin-Demers and Weatherhead 2001) and thermal exploitation (E_x) (Christian and Weavers 1996), one can perform a

relatively complete evaluation of thermoregulation in field-active small reptiles for virtually any ecological situation.

1.1.5 The cost-benefit model of thermoregulation (Huey and Slatkin 1976)

The cost-benefit model of thermoregulation states that thermoregulatory investment will be abandoned if the costs exceed the benefits (Huey and Slatkin 1976). The costs of thermoregulation is however associated with thermal habitat quality since ultimately, thermoregulatory requirements are a function thereof (Blouin-Demers and Nadeau 2005) and not surprisingly comprise the predominant factor associated with macro-scale variation in thermoregulatory success (among populations or seasonally) (e.g. Hertz *et al.* 1993; Angilletta 2001). In fact, Herczeg *et al.* (2006) found that *Lacerta vivipara* individuals abandoned thermoregulation when exposed to temperatures below the specie's T_p in support of the cost-benefit model. Costs of thermoregulation include predation risk (Herczeg *et al.* 2008), social behaviour such as mating and courtship (Herczeg *et al.* 2008) and feeding behaviour (Hertz *et al.* 1993). The actual model proposed by Huey and Slatkin (1976) mainly focuses on thermal quality as determinant of thermoregulatory cost, seeing that actual costs such as predation risk or social behaviour are difficult to quantify and would require a more complex model (Blouin-Demers and Weatherhead 2002).

A recent application of the Hertz *et al.* (1993) protocol is in studies exploring the legitimacy of the cost-benefit model of thermoregulation in a field setting (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Weatherhead 2002; Blouin-Demers and Nadeau 2005). Since the cost-benefit model (Huey and Slatkin 1976) predicts that thermoregulatory behaviour will be abandoned when thermal habitat quality is low (cost of thermoregulation outweighs the benefit), one can compare the observed extent and success of thermoregulation to the prevalent thermal habitat quality in order to see whether animals thermoregulate in accordance with the cost benefit model (i.e. abandon thermoregulation when exposed to temperatures below the species preferred temperature range (Herczeg *et al.* 2006)).

Certain reptiles from extreme cold temperate regions such as northern Canada have been reported to thermoregulate in conflict with the predictions of cost-benefit model of thermoregulation (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Weatherhead 2002; Row and Blouin-Demers 2006; Edwards and Blouin-Demers 2007). For example, Blouin-Demers and Weatherhead (2001) found that the snake, *Elaphe obsoleta* thermoregulates behaviourally, even though the operative environmental temperatures in its habitat were below the specie's T_p, and in fact, invest more in thermoregulation in low quality habitats (in contrast to the predictions of the Huey and Slatkin (1976) model). Blouin-Demers and Weatherhead (2001) suggested that the disadvantages (costs) of thermoconformation in this cold environment may exceed the cost of thermoregulation and *E. obsoleta* would still benefit from active thermoregulation. The question however remains, does the Blouin-Demers and Weatherhead (2001) model apply to reptiles occurring in hot habitats where the risk of overheating poses a problem to animals, since the disadvantages of remaining in retreat-sites may also be substantial. In a meta-analysis (33 species from variable climatic regions) Blouin-Demers and Nadeau (2005) observed a general trend for reptiles to exhibit increased thermoregulatory investment (described by the effectiveness of thermoregulation index) in higher cost (low thermal quality) habitats.

1.2 Thermal ecology of the Cordylidae family

The field of reptile thermal ecology has proliferated since the ground-breaking contributions of Cowles and Bogert (1944) describing the presence of behavioural thermoregulation, Heath (1964) who identified operative environmental temperatures, Licht *et al.* (1966) on the existence of a target preferred temperature range, and Huey and Slatkin (1976) who conceptualized reptile energy balance in relation to thermoregulation. Nonetheless, surprisingly few published records of thermal biology in the African-endemic Cordylidae family exists, of which only one applied the Hertz *et al.* (1993)-protocol (i.e. Clusella-Trullas *et al.* 2009).

Here follows a short description of published records related to the respective subject fields of field thermal ecology and thermal physiology in cordylids.

1.2.1 Field thermal ecology

Stebbins (1961) measured the body temperatures of *Gerrhosaurus flavigularis* in outdoor enclosures during summer and reported typical basking behaviour and a mean T_b of 33.3^oC. Stebbins (1961)'s initial aim was to describe the effect of the parietal eye on thermoregulation, and observed no effect associated with the removal of the eye.

Bowker (1984) measured the body temperatures for *Gerrhosaurus major* and *Gerrhosaurus nigrolineatus* in outdoor enclosures, and observed the highest T_bs reported among cordylids to date (i.e. *G. major* 34.5^oC; *G. nigrolineatus* 35.2^oC). Bowker (1984) further reported that both *G. major* and *G. nigrolineatus* performed overt thermoregulatory behaviour, shuttling between sun and shade when needed.

Bauwens *et al.* (1999) explored the thermal habitat and field body temperatures of *Cordylus macropholis* (a species which inhabits the *Euphorbia caput-medusa* plant on the West Coast of South Africa) and reported the absence of overt thermoregulatory activity such as shuttling and basking, implicating *C. macropholis* as a thermoconformer. Bauwens *et al.* (1999) described low field T_bs (mean 28.9^oC) during summer, and suggested that *E. caput-medusa* plants provide superior opportunities for thermoregulation compared with shrub microhabitats. Bauwens *et al.* (1999)'s estimates of thermal suitability were however based simply on ambient temperatures among plant leaves and not environmental operative temperatures, therefore compromising the credibility thereof (Heath 1964).

Lailvaux *et al.* (2003) measured the field body temperatures of *Platysaurus intermedius wilhelmi* during summer, specifically testing for inter-sexual variation, and reported significantly higher T_bs in males than females.

Clusella-Trullas *et al.* (2009) applied the Hertz *et al.* (1993) protocol and comprehensively described the thermal habitats and subsequent thermoregulatory patterns of *Cordylus oelofseni*, *Cordylus niger* and *Cordylus cordylus* populations. The specific focus

of Clusella-Trullas *et al.* (2009)'s study was to investigate thermal benefits of melanism, and the authors concluded that melanism confers only a slight, but significant thermoregulatory advantage to lizards in cool locations (montane and coastal areas) during cool periods, allowing increased heating rates and higher T_b.

Finally, in the most recent paper, McConnachie *et al.* (2009) provided a detailed description of behavioural thermoregulation in *Pseudocordylus melanotus melanotus* in relation to postural adjustments and movement during summer and winter. Although McConnachie *et al.* (2009) reported operative environmental temperatures (T_e) and field body temperatures (T_b), the accuracy or effectiveness of thermoregulation (Hertz *et al.* 1993) was not given.

In summary, field thermal ecology represents a large knowledge gap in cordylid literature, with a specific need for basic descriptive studies related to the thermal quality of habitats and thermoregulatory strategies adopted by lizards. In addition, virtually no published work describing seasonal patterns of thermoregulation, or making population-level comparisons on thermal ecology currently exists. Moreover, fine scale (micro-spatial) exploration of thermal habitats of cordylids (see Huey *et al.* 1989; Kearney 2002) are non-existent and represents a major gap, since the family predominantly consists of sedentary sit-and-wait foragers (Branch 1998) which are expected to be influenced by microsite level variation in T_e, in and around crevices (due to the individuals' site specificity) (Huey *et al.* 1989; Kearney 2002). The lack of descriptive thermal ecology studies also precludes the use of modelling effects on climate change (Kearney *et al.* 2009).

1.2.2 Thermal physiology

Wheeler (1986) measured standard metabolic rate (SMR) and preferred body temperatures (T_p) of *Cordylus jonesi* in individuals respectively acclimated at 20 ^{o}C and 30 ^{o}C for five weeks. The SMR of *C. jonesi* showed a compensation of 20.9 %, but T_p remained unchanged. Wheeler (1986) further noted that SMRs of lizards that were allowed to bask at day-time corresponded to that of individuals forced to remain in retreat, suggesting that the

acclimation state of lizards was determined by body temperatures experienced whilst in retreat (during scotophase).

Skinner (1991) explored the effect of melatonin injections on the thermal preference of *Cordylus vittifer* and reported significantly lower T_bs in exposed individuals, implicating melatonin as an important seasonal trigger for altered thermoregulatory responses in these lizards. Skinner further reported that individuals (injected and uninjected with melatonin) selected higher T_bs in a thermal gradient during the scotophase than photophase.

McKinon and Alexander (1999) measured apparent digestive efficiency (ADE) in *Platysaurus intermedius* when fed with low and high quality food at 26 ^{o}C and 31 ^{o}C respectively. The apparent digestive efficiency *P. intermedius* was lower in low quality diets, yet did not vary among temperature classes for low and high quality diets.

Mouton *et al.* (2000b) assessed the resting metabolic rates (RMR) of *Cordylus cataphractus* and *Cordylus polyzonus* at 10 ^{o}C, 15 ^{o}C, 20 ^{o}C, 25 and 30 ^{o}C and reported a degree of thermally independent metabolism and highly repressed RMR in *C. cataphractus*, 74 % lower than that observed in *C. polyzonus* at the 30 ^{o}C exposure.

Alexander *et al.* (2001) described the thermal dependence of appetite and digestive rate on *Platysaurus intermedius wilhelmi*. Appetite was temperature dependent, maximized at 32 ^{o}C, whereas digestive rate was found to be influenced by T_bs lower than 22 ^{o}C, yet independent beyond 22 ^{o}C and 34 ^{o}C. The authors concluded that *P. i. wilhelmi* requires T_bs of at least 20 ^{o}C to gain energy through food consumption.

Lailvaux *et al.* (2003) assessed sexual variation in locomotor performance, thermal preference (T_p) and escape behaviour in *Platysaurus intermedius wilhelmi*, and reported significantly higher sprint speeds in males. Lailvaux *et al.* (2003) provides the only record of thermal performance curves for a cordylid. Interestingly, the T_{opt} for sprinting corresponded closely to mean T_p being 31.9 ^{o}C and 31.2 ^{o}C respectively.

McConnachie and Alexander (2004) described the effects of temperature on apparent digestive efficiency, apparent assimilation efficiency, gut passage time and appetite in *Pseudocordylus melanotus melanotus*. Apparent digestive and apparent assimilation

efficiencies were high (i.e. 94.4 % and 87.2 % respectively) both being temperature independent, whereas increases in temperature resulted in increased appetite and decreased gut passage time. Lizards are therefore assimilating a similar proportion of ingested energy, yet more rapidly at higher temperatures. The authors concluded that the digestive physiology of *P. m. melanotus* allows maximum energy gain in food scarce regions.

McConnachie *et al.* (2007) estimated the thermal tolerance (i.e. the lower lethal temperature and critical thermal minimum) of *Pseudocordylus melanotus melanotus*. A lower lethal temperature of $-5.2\ ^{o}$C was observed, whereas the critical thermal minimum (CT_{min}) was $10.2\ ^{o}$C, an unexpectedly high value since these lizards are known to frequently reach lower T_{b}s during winter (McConnachie *et al.* 2007).

Clusella-Trullas *et al.* (2007) explored the thermal preferences of *Cordylus oelofseni*, *Cordylus polyzonus*, *Cordylus niger* and *Cordylus cordylus* during summer, with the specific outcome of investigating among and within subject repeatability (defined as the intra-class correlation coefficient) in T_{p}. Repeatability of T_{p} was low in all species investigated in comparison to values reported for other species in the literature (Clusella-Trullas *et al.* 2007). In conclusion, Clusella-Trullas *et al.* (2007) suggested that the low repeatability was a result of real random biological variation in the species under investigation.

Clusella-Trullas *et al.* (2009) described the critical thermal maxima and minima of *Cordylus oelofseni*, *Cordylus niger* and *Cordylus cordylus*. The CT_{min} of *C. oelofseni* was significantly lower than that of both *C. niger* and *C. cordylus*, whereas CT_{max} did not vary significantly among species. Interestingly, the CT_{min} of *Pseudocordylus melanotus melanotus* exceeded the CT_{min}s of all three species investigated by Clusella-Trullas *et al.* (2009), even though the latter species are known to experience less extreme T_{b}s in nature (Clusella-Trullas *et al.* 2009; McConnachie *et al.* 2009).

Finally, the most recent contribution was made by McConnachie *et al.* (2009) who described the preferred body temperature range (T_{p}) of *Pseudocordylus melanotus*

melanotus during summer and winter, and reported a significantly lower T_p during winter than summer.

In summary, although thermal physiology is one of the best studied subject fields in Cordylidae, major gaps still exists. In particular, basic descriptive thermal physiology studies are needed in the numerous unexplored species (e.g. thermal dependence of metabolic functioning or digestion). Other topics such as the thermal dependence of growth rates, -reproduction, -sex determination, and -water balance remains unexplored. Thermal performance curves, which have been described in only one study to date (Lailvaux *et al.* 2003), are also lacking, and the exploration of physiological traits at seasonal scale is limited (McConnachie *et al.* 2009), whereas, population level studies are nonexistent.

1.3 *Cordylus cataphractus* and the group-living life strategy

Cordylus cataphractus inhabit the semi-arid far western parts of South Africa occurring in permanent social groups of between two and 50+ individuals (Mouton *et al.* 1999; Visagie *et al.* 2005; Effenberger and Mouton 2007). Stable social aggregations are uncommon in squamates (Hayward 2008) and has generally been associated with two mutually non-exclusive factors namely (1) mutual attraction of conspecifics (phylopatry: i.e. an animal benefits from being in the close proximity of conspecifics) and (2) ecological constraints such as limitations in retreat sites, food availability or mates (Stamps 1988; Graves and Duvall 1995; Kearney *et al.* 2001; Hayward 2008). *Cordylus cataphractus* exhibits one of the clearest manifestations of the group-living life strategy among squamates (Visagie *et al.* 2005; Hayward 2008), and preferentially aggregate even when provided with an excess of food and retreat sites, suggesting phylopatric association (Visagie *et al.* 2005). *Cordylus cataphractus* is a rock dwelling insectivore and primarily employs a sit-and-wait foraging mode (Mouton *et al.* 2000a). Social groups may host numerous highly territorial males which typically occupy rock sections of ~0.79 m^2 (Effenberger and Mouton 2007). *Cordylus cataphractus* relies on crevices as primary defence mechanism, and therefore rarely move further than 0.9 m away from native rocks (Losos *et al.* 2002; Effenberger and Mouton

2007). Osteo-dermal armature as well as thickened bones results in low manoeuvrability, further contributing to their general site specificity and placid behaviour (Visagie 2001; Hayward and Mouton 2007; Hayward 2008).

The unique combination of site specificity, semi-arid habitat, group-living life strategy and a sit-and-wait foraging mode creates a unique and challenging scenario resulting in high expected levels of competition for food during dry periods. Mouton *et al.* (2000a) observed empty stomachs in 64 % of individuals collected during the dry autumn (*N* = 91 specimens), confirming amplified seasonal food stress in the species.

Parturition typically occurs during the dry late summer and autumn months in *C. cataphractus* (February to April), after which vitellogenesis commences, continuing until summer (April to December) (Flemming and Mouton 2002). Spermatogenesis typically commences during midsummer and continues until spring (December to October) (Flemming and Mouton 2002). The mating season of *C. cataphractus* occurs predominantly during spring, yet may continue until midsummer (Flemming and Mouton 2000). Interestingly, both vitellogenesis and spermatogenesis occur during the annual period when the surface activity of *C. cataphractus* reportedly is repressed (February to July) (Visagie 2001). Effective thermoregulation will therefore benefit individuals at the time, despite repressed activity (Licht 1972).

Cordylus cataphractus exhibits several characteristics uncommon among cordylids, including: a degree of thermally independent metabolism and low resting metabolic rate (RMR), 68.8 % lower than that of any other known cordylid (Mouton *et al.* 2000b); enlarged fat bodies principally deposited during spring (three times larger than most other cordylids) (Flemming and Mouton 2002), low fecundity (a single offspring per annum) (Flemming and Mouton 2002), termitophagy during the dry summer and autumn months as well as the cool winter (Shuttleworth *et al.* 2008) and as mentioned, repressed annual activity cycles, from summer to autumn (Visagie 2001). These aforementioned features have generally been ascribed to food constraints associated with the combination of a sit-and-wait foraging mode and permanent group-living in a semi-arid to arid context (Mouton *et al.* 2000a; Visagie

2001; Hayward 2008; Flemming and Mouton 2002; Shuttleworth *et al.* 2008). Other processes such as thermoregulation are likely to also be influenced.

Cordylus cataphractus is probably the best studied cordylid, and accounts exists describing the species in relation to: morphology (Mouton *et al.* 1999; Curtin *et al.* 2005), sexual dimorphism (Mouton *et al.* 1999), feeding strategy (Mouton *et al.* 2000a; Shuttleworth *et al.* 2008), physiology (Mouton *et al.* 2000b; Flemming and Mouton 2002), grouping behaviour (Mouton *et al.* 1999; Visagie *et al.* 2002; Visagie *et al.* 2005; Costandius *et al.* 2006), activity patterns and territoriality (Effenberger and Mouton 2007).

Thermal ecology however represents a current gap in the literature on *C. cataphractus*. It is imperative (because of ectothermy) to consider thermal ecology when exploring and interpreting behavioural and physiological processes operational in reptiles (Huey 1982; Angilletta 2009), and a better understanding thereof will therefore complement the current knowledge-base available for *C. cataphractus*.

In a preliminary study, Truter (2007) reported a T_p of 30.1 ^{o}C which is the lowest reported among cordylids to date, and suggested the low T_p as a consequence of the group-living life strategy in a semi-arid environment. Truter (2007) also provided an initial basic description of the thermal habitat of *C. cataphractus* during spring and suggested that individuals performed active (behavioural) thermoregulation to reach preferred body temperatures.

Since previous studies indicate strong seasonal effects in regard to activity patterns (Visagie 2001), reproductive cycles (Flemming and Mouton 2002) resource availability (Mouton *et al.* 2000a) and feeding behaviour (Shuttleworth *et al.* 2008), the exploration of seasonality in thermoregulatory patterns as well as the thermal habitat is important for *C. cataphractus*. Moreover, the distribution range of *C. cataphractus* stretches from the South African West Coast, to inland regions such as the more mountainous Cederberg Wilderness Area (Branch 1998). Although *C. cataphractus*' distribution range is limited to the winter rainfall regions (Shuttleworth 2006), vegetation types and stochastic factors may vary remarkably among regions (Mucina and Rutherford 2006), and thermal ecology of

populations inhabiting different locations may therefore differ and will be meaningful to explore.

Moreover, permanent group-living is expected to impact the cost-benefit balances of reptiles and therefore thermoregulation. This effect may be pronounced in *C. cataphractus* due to prolonged periods of low food availability (Mouton *et al.* 2000a; Hayward 2008) and the potentially large groups they occur in (Mouton *et al.* 1999). Group-living has been shown to confer thermal benefits in certain reptile species (Boersma 1982; Lanham 2001; Shah *et al.* 2003). However, in *C. cataphractus*, the effects of living in groups on thermoregulation (positive and/or negative) remain unexplored.

In addition, a better understanding of the thermal ecology of *C. cataphractus* will aid in formulating effective conservation/management plans, specifically in consideration of global climate change (Porter *et al.* 2002; Kearney *et al.* 2009). Such an outcome is of merit since *Cordylus cataphractus* is listed as *Vulnerable* in the South African Red Data Book for Reptiles and Amphibians (Branch 1988) as well as by the International Union for the Conservation of Nature's Red list of Threatened Animals (Groombridge and Baillie 1997) due to its attractive appearance, group-living life strategy and subsequent popularity as pet.

1.4 Study Aims

In this study the thermal ecology of *Cordylus cataphractus* was explored at both spatial and temporal scales. The spatial assessment was performed at macro- (population) and micro- (microhabitat) scales, whereas the temporal assessment was performed at diel and seasonal scales.

The main objectives of the current study were:

1. To describe the preferred temperature range (T_p) of *C. cataphractus* with specific reference to seasonal (autumn versus spring) and geographical variation (coastal versus inland), therefore testing for temporal and spatial plasticity in T_p.

2. To explore seasonality in the thermal habitat and patterns of thermoregulation of *C. cataphractus*, by investigating a single population during summer (January), autumn (April), winter (July) and spring (September).

3. To investigate micro spatial variation of operative environmental temperatures (i.e. around and beneath rocks) in a population of *C. cataphractus* during summer, autumn, winter and spring.

4. To investigate population level variation in the thermal habitat and patterns of thermoregulation in *C. cataphractus* (coastal versus inland).

A compilation of thermoregulatory indices were used to quantitatively describe thermal ecology in relation to:

1. Accuracy of thermoregulation (Hertz *et al.* 1993)

2. Thermal habitat quality (Hertz *et al.* 1993)

3. Effectiveness of thermoregulation (Blouin-Demers and Weatherhead 2001)

4. Thermal exploitation (Christian and Weavers 1996)

The specific questions addressed by the study included:

1. Does the preferred temperature range of *C. cataphractus* vary geographically among an inland and coastal population during the dry autumn and more mesic spring?

2. Do laboratory photo-thermal gradients provide estimates of preferred body temperatures that are repeatable across days?

3. How does the thermal habitat quality of *C. cataphractus* vary at micro-spatial scale (i.e. around rocks) as a function of the time of day and time of year (i.e. season)?

    Does variation in thermal habitat quality around rocks provide an incentive for intra group competition?

4. Does the success and effectiveness of thermoregulation vary seasonally among summer, autumn, winter and spring in *C. cataphractus*?

5. Are the seasonal surface activity patterns on rocks previously reported for *C. cataphractus* related to thermal factors?

6. Does the thermal habitat quality of *C. cataphractus* and effectiveness and success of thermoregulation vary among an inland and coastal population during dry autumn and more mesic spring as predicted by climatic data?

7. Does the success and effectiveness of thermoregulation of *C. cataphractus* vary seasonally in response to the relative thermal quality as predicted by the cost-benefit model of thermoregulation, or is thermoregulation dictated by the amplified energy constraints related to group-living?

Chapter 2

Thermal preference across seasonal and geographical boundaries in the group-living lizard, *Cordylus cataphractus*

2.1 Abstract

Most reptiles possess a dual set-point range of body temperatures known as the preferred temperature range (T_p), at which biological functioning is optimized (i.e. the target of thermoregulation). Seasonal variation in preferred body temperatures is common among squamates, occurring in response to thermal regimes or food availability. In contrast, population-level variation in T_p is virtually non-existent. Although T_p has been estimated in a number of cordylids, seasonal variation in this parameter is known for only one, and population-level variation remains unexplored. The preferred temperature range of the group-living armadillo girdled lizard *Cordylus cataphractus* was estimated during the respective annual peak periods in food availability and scarcity. Measurements were taken in ecologically realistic laboratory photo-thermal gradients across 13 days using modified Thermochron iButtons. The aims were: (1) to characterize T_p for *Cordylus cataphractus* and compare the results to the T_ps known for other (non-group-living) cordylids; (2) to assess geographical variation in T_p; (3) test for phenotypic plasticity in T_p at a seasonal scale. The grand mean T_p among populations and across seasons was 29.8 ^{o}C and represents the lowest T_p recorded for any cordylid to date. There was no significant variation in T_p at both seasonal and geographic scale, suggesting the absence of acclimatization (physiological plasticity) in response to seasonal temperature flux. The among-day repeatability of mean T_p varied among populations and across seasons despite the fact that exposure conditions were kept constant, suggesting that the methodology for T_p estimation does not implicitly describe the physiological target body temperature range. *Cordylus cataphractus* is known to rarely emerge from crevices during the dry autumn. The current results show that lizards

actively exploited thermal opportunities in laboratory thermal gradients during autumn (although to a lower extent than in spring); therefore indicating that lizards will if needed emerge from crevices for thermoregulatory purposes.

Key words: Preferred temperature range, seasonal variation, geographic variation, food constraints.

2.2 Introduction

Body temperature (T_b) is an important factor related to all biochemical processes and higher levels of organization (Haynie 2001; Angilletta *et al.* 2006). In most reptiles, biological processes function at an optimal level within a range of T_bs known as the preferred temperature range (T_p) (Stevenson *et al.* 1985; Angilletta *et al.* 2002; Martin and Huey 2008). Thermoregulation functions to achieve and maintain body temperatures (T_b) as close as possible to this target preferred temperature range (T_p), thus ensuring optimal biological functioning. Knowledge regarding such a target range of T_bs is essential for evaluating lizard thermal ecology (Hertz *et al.* 1993; Bauwens *et al.* 1996; Clusella-Trullas *et al.* 2009).

The multidimensional relationship between body temperatures, the environmental heat resource and fitness (through physiological temperature dependency) makes thermoregulation one of the central paradigms of reptile (ectotherm) ecology (Martin and Huey 2008; Angilletta 2009). Reptile thermoregulation is principally facilitated behaviourally through microsite selection, shuttling, selective inactivity, postural adjustments and orientation (Bauwens *et al.* 1996; Webb and Shine 1998; Kearney and Predavec 2000), but also physiologically through cardiovascular mechanisms such as altered blood flow (i.e. vasodilatation or vasoconstriction), or metabolic heat production (Bartholomew 1982). In reptiles, thermoregulatory behaviour incurs either a time or energy cost to the animal (Huey and Slatkin 1976), which varies along a continuum, with low cost (basically thermoconformation) and high cost (active thermoregulation) on the other end (Huey 1982). The extent of such thermoregulatory costs is directly related to the degree to which available body temperatures (i.e. operative environmental temperatures) deviate from T_p (the target T_b range) (i.e. thermal habitat quality (Hertz *et al.* 1993)) (Huey and Slatkin 1976). The T_p of any species, therefore potentially affects the costs associated with thermoregulation if one assumes that the time spent within preferred temperatures represent optimal functioning in the species.

Although T_p is generally variable at genus level (Angilletta and Werner 1998), related species typically have corresponding T_ps (Licht *et al.* 1966; Huey 1982; Angilletta and

Werner 1998; Kohlsdorf and Navas 2006). Similarly, T_p may be highly conservative at population level despite the fact that populations occur across diverse thermal habitats such as along altitudinal gradients (Gvozdik and Castilla 2001; Diaz *et al.* 2006). In fact, only one report of geographic variation has been published (Du 2006) and static T_p among populations seems to be the rule rather than the exception. The invariable T_p at population level is expected to result in variable thermoregulatory costs among populations (functional to thermal characteristics) (Huey and Slatkin 1976) and may therefore have substantial effects on time and energy budgets (Gvozdik and Castilla 2001; Gvozdik 2002).

In contrast, several reports of seasonal variation in T_p exist (e.g. Patterson and Davies 1978; Van Damme *et al.* 1986; Firth and Belan 1998). Such seasonal variation in T_p may counteract seasonal increases in thermoregulatory costs, since T_p may shift towards the prevalent environmental temperatures (e.g. increase T_p during summer) (Van Damme *et al.* 1987; Diaz and Cabezas-Diaz 2004; McConnachie *et al.* 2009). Such shifts are facilitated through acclimatization (reversible phenotypic/physiological plasticity) which alters the biochemical reaction rates of temperature dependent processes, changing the optimum biological temperatures and hence T_p (Seebacher 2005).

Seasonal variation in T_p has also been suggested to be associated with food and water availability (Huey and Slatkin 1976; Christian *et al.* 1996; Christian and Bedford 1996; Seebacher 2005). Animals can in such cases employ acclimatization to simply lower T_p (irrespective of environmental temperatures); therefore, because of the thermodynamic rate dependence of biological functions (Haynie 2001), lowering basal metabolic expenditure and water flux (Christian and Bedford 1995; Christian and Bedford 1996; Seebacher 2005).

If T_p does indeed vary seasonally and/or geographically, one would expect such variation in cases of either extreme variation in temperature or food availability, or in species with extremely strict energy budgets which in turn would benefit from minimized thermoregulatory costs.

Cordylus cataphractus is a permanent group-living sit-and-wait forager (Mouton *et al.* 1999; Mouton *et al.* 2000a) that inhabits the semi-arid far-western parts of South Africa

(Mouton *et al.* 1999). Individuals occur in permanent social groups of up to 58 (and possibly more) and rarely move further than 0.9 m from their native crevices (Mouton *et al.* 1999; Visagie *et al.* 2005; Hayward 2008). The unique combination of extreme site specificity, a semi-arid habitat, a group-living life strategy and a sit-and-wait foraging mode contribute to seasonal food stress during dry periods (Mouton *et al.* 2000a; Hayward 2008). This phenomenon peaks at the end of the warm dry season (i.e. late summer to autumn, February to April), and is least in spring when perennial flower blooms sustain an abundance of invertebrates (Struck 1994; Mouton *et al.* 2000a; Visagie 2001; Hayward 2008). It may be predicted that *Cordylus cataphractus* individuals will therefore benefit from reduced thermoregulatory costs appropriated through seasonal variation in T_p.

A number of characteristics exhibited by *C. cataphractus* (absent in most other cordylids) have been suggested to be associated with their group-living life strategy; to aid survival during prolonged periods of food scarcity, namely: (1) a low resting metabolic rate (and therefore internal heat production) (Mouton *et al.* 2000b); (2) enlarged fat bodies, the largest in proportion to body size observed among cordylids (Flemming and Mouton 2002); (3) seasonal termitophagy (Shuttleworth *et al.* 2008); (4) reduced litter size, a single offspring per annum (Flemming and Mouton 2002) and (5) repressed seasonal outside crevice / rock surface activity (Visagie 2001).

Few researchers have explored thermal preference in cordylids (Wheeler 1986; Skinner 1991; Lailvaux *et al.* 2003; Clusella-Trullas *et al.* 2007; Janse van Rensburg 2009; McConnachie *et al.* 2009), of which seasonal variation in T_p was exclusively explored in *Pseudocordylus melanotus melanotus* (McConnachie *et al.* 2009), and population level variation of T_p remains unexplored.

In a preliminary study, Truter (2007) estimated the preferred temperature range of a population of *C. cataphractus* and reported a mean T_p of 30.1°C, the lowest reported among cordylids to date (Clusella-Trullas *et al.* 2007). Truter (2007) identified the need to investigate the effects of temporal (seasonal) and spatial (geographic) variation in

environmental thermal quality and associated costs of thermoregulation in a group-living species like *C. cataphractus*.

Clusella-Trullas *et al.* (2007) investigated thermal preference in four cordylids (*Cordylus cordylus*, *Cordylus niger*, *Cordylus oelofseni* and *Cordylus polyzonus)*, with the specific outcome of assessing repeatability (i.e. the intraclass correlation coefficient) thermal preference (T_p). These authors observed low repeatability in all four species investigated (from 0 to 0.48) in comparison to other estimates of repeatability of T_p in the literature (Galliard *et al.* 2003). The low repeatability indicates that the inter-individual variance of T_p was inconsistent over time and low in proportion to intra-individual variance of T_p (Sokal and Rohlf 1981). Clussella-Trullas *et al.* (2007) identified the need for future studies which assess repeatability in T_p in cordylids over different time scales (e.g. seasons) among species and between diverse geographic and climatic conditions (i.e. populations).

The use of laboratory thermal gradients to estimate the preferred temperature range of reptiles has been criticized, specifically due to the assumption that laboratory thermal gradients represent a zero cost environment (Christian and Weavers 1996; Currin and Alexander 1999). If costs are indeed zero in laboratory thermal gradients, estimates of T_p over time are expected to be relatively consistent within and among individuals and therefore have high repeatability. The low repeatability observed by Clussella-Trullas *et al.* (2007) brings the legitimacy of T_p as representative of the "set point" target temperature range into question. Clusella-Trullas *et al.* (2007) recorded T_p in laboratory thermal gradients which lacked retreat sites even though the species investigated are known to rely on crevices as primary defence mechanism in nature (Losos *et al.* 2002). Ecologically realistic photo-thermal gradients may result in higher repeatability (since natural behaviour will be encouraged) and therefore more realistic estimates of T_p, however, the matter currently remains unexplored.

The primary objective of the current study was to describe the preferred temperature range of the group-living *C. cataphractus* at spatial and temporal scales, studying two

populations (a coastal and an inland population) during two important seasons (warm autumn and cooler spring).

Specific questions addressed:

1. Does the preferred temperature range of *C. cataphractus* vary geographically among an inland and coastal population during dry autumn and more mesic spring?

2. Does the preferred temperature range of *C. cataphractus* vary seasonally as a function of annual food availability?

3. Does *C. cataphractus* perform overt thermoregulatory behaviour during the dry autumn when activity is known to be largely confined to the crevices?

4. Does the repeatability of T_p in *C. cataphractus* vary at seasonal and temporal scales and correspond to values obtained for other cordylids?

2.3 Materials and Methods

2.3.1 Study area and animals

Lizards were captured from a coastal and inland population of *C. cataphractus* during the autumn (April) and spring (September) of 2008. The coastal population inhabits a series of sandstone ridges near Elands Bay (Western Cape, South Africa (32°19'38.61"S; 18°21'35.78"E)), which falls within the Langebaan Dune Strandveld vegetation region, with an annual precipitation of 200 mm (South African Weather Service) (Figure 2.1). The coastal locality is densely populated by *C. cataphractus* with group-sizes varying between two and 25 individuals (Visagie 2001).
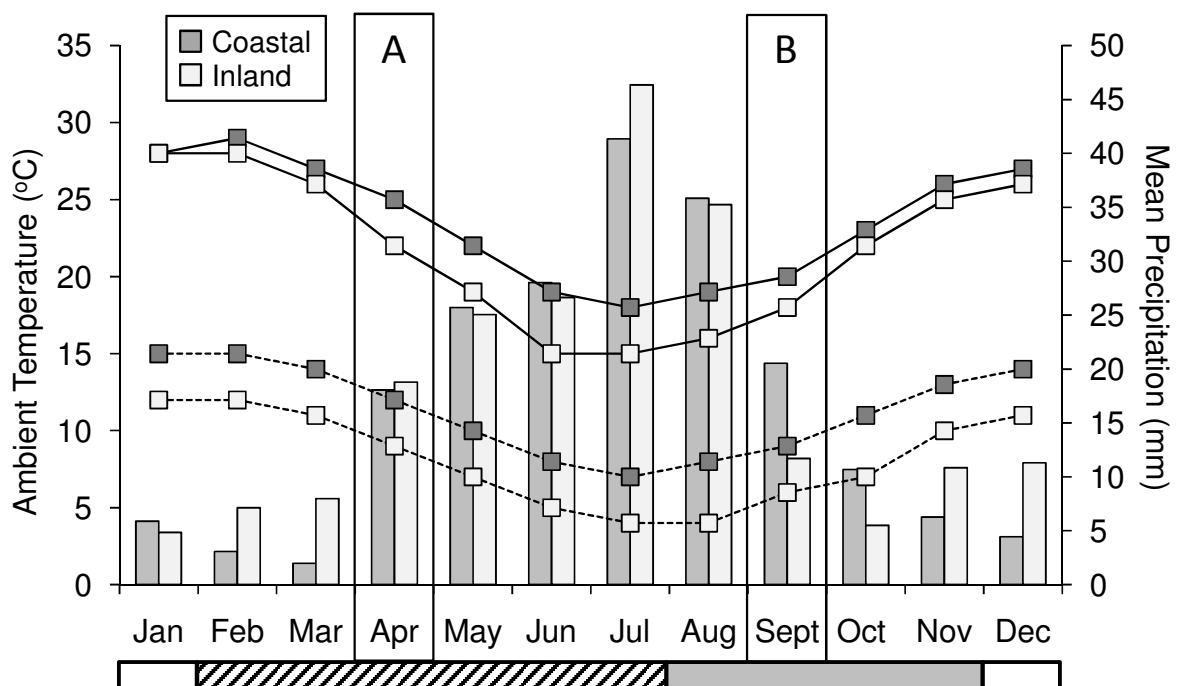
Figure 2.1. Mean monthly rainfall (vertical bars), minimum and maximum ambient temperatures (lines) for the coastal (dark grey) and inland (light grey) localities (rainfall: 1998-2008, SA Weather Services; temperatures and solar radiation (A van Niekerk, unpublished data)). Vertical bars indicate the respective sampling periods (A: autumn; B: spring). The horizontal bar indicates seasonal activity in *C. cataphractus* as described in the literature (Visagie 2001; Effenberger and Mouton 2007) (slanted-line: repressed activity; grey: normal activity; clear: activity unknown).

The inland population is located in the Matjiesrivier Nature Reserve (Western Cape, South Africa (32°29'01.53"S; 19°21'31.18"E)), ~120km south-east of the coastal population. The site has an annual precipitation of 210 mm (South African Weather Service) (Figure 2.1). The area is scattered with quartzite sandstone boulders that provide the ideal habitat for *C. cataphractus*, yet; population density is low, with a maximum-recorded group-size of six (Retief 2000).

2.3.2 Laboratory experiment

2.3.2.1 Experimental design

Seven *C. cataphractus* individuals were captured at each of the two localities and transported to the laboratory within two days. All individuals were released at the exact point of capture after the experiment had ended. The aim was to use the same lizards during both seasons. One individual from Elands Bay and two from the Matjiesriver study areas could however not be retrieved during the second trial and substitutes had to be used in the following season. The animals were housed in wooden terrariums placed in a controlled environmental chamber (20 °C ± 1.5 °C) under natural daylight regimes (12:12 L:D in autumn and spring) typical for autumn and spring. Because these lizards naturally occur in social groups (Mouton *et al.* 1999) and are known to preferentially aggregate even though an excess of favourable retreat sites are available (Visagie *et al.* 2005), a minimum of two and a maximum of four individuals captured from the same group were allocated per terrarium to reduce stress. The terrariums were constructed, as to mimic natural conditions, each containing a single crevice, and a base consisting of small rocks (diameter: ~1 mm – 3 mm) and sandstone slates. Terrarium sizes matched the natural movement patterns of *C. cataphractus* (0.9 m x 0.45 m x 0.3 m [length, width, height] for housing groups of two and 0.9 m x 0.9 m x 0.3 m for housing groups of more than two individuals) (Effenberger and Mouton 2007).

The smaller terrariums were fitted with one and the larger terrariums with two 250 W infrared bulbs positioned 0.5 m from the ground at the end opposite the crevice, generating a

photo-thermal gradient with operative environmental temperatures (T_e) ranging from 55 ^{o}C to 22 ^{o}C. The IR bulbs were activated for 12 hours each day (7h00 – 19h00). Lizards remained in the terrariums for the full duration of the 14 day experimental trial. Food (*Tenebrio molitor* larvae) and water were supplied approximately every 48 h, after 18h00, thus minimizing human contact to the animals.

2.3.2.2 Modified iButton temperature loggers

Robert and Thompson (2003) described a technique to modify iButton temperature loggers (iButton; Maxim, USA). By removing the electronic contents from its stainless steel casing and then coating it with Plasti Dip (Performix, USA), both the size and weight is reduced. These loggers can be attached to the skin surface of small vertebrates and (because of the animal's low heat capacity) provide a realistic estimate of internal body temperature (Robert and Thompson 2003).

By rearranging the electronics, the technique described by Robert and Thompson (2003) was further modified, resulting in an even thinner logger (Figure 2.2). The thickness was reduced by 37 % (from 6 mm to 3.8 mm), whereas mass was reduced by 46 % (modified iButton: 1.75 g), which were at most 5.8 % of the current study subjects' body mass. The use of modified iButtons, instead of the conventional trailing (cloacal) thermocouples or "grab and jab" (quick reading thermometer) techniques, promote natural behaviour because it does not hamper movement and eliminates direct human contact during trials. The loggers were attached to the dorsal body surface of each lizard with super glue gel (Henkel, RSA), and remained attached for the full duration of the study.

Figure 2.2. An adult male *C. cataphractus* from the Matjiesriver inland population fitted with a modified iButton temperature logger.

Three iButton-carrying lizards from each population were fitted with cloacal temperature probes (K-type thermocouple, inserted ~10 mm deep) in order to assess how closely modified-iButton (surface) temperatures reflect internal body temperatures. The animals were secured on isolative cardboard sheets, placed beneath two 500 W halogen spotlights which were collectively positioned at a series of corresponding heights. Equilibrium temperatures recorded at the exact same time for each light intensity could thus be compared. The degree of correlation was assessed through a standard linear regression (r = 0.97, R^2 = 0.93; iButton = 1.04 T_b – 0.92; Figure 2.3). Theoretically, a slope of one and an intercept of zero indicate a perfect correlation.

The regression function was subsequently employed to adjust all T_bs recorded throughout the study, thus correcting for the difference between iButton and internal body temperature.
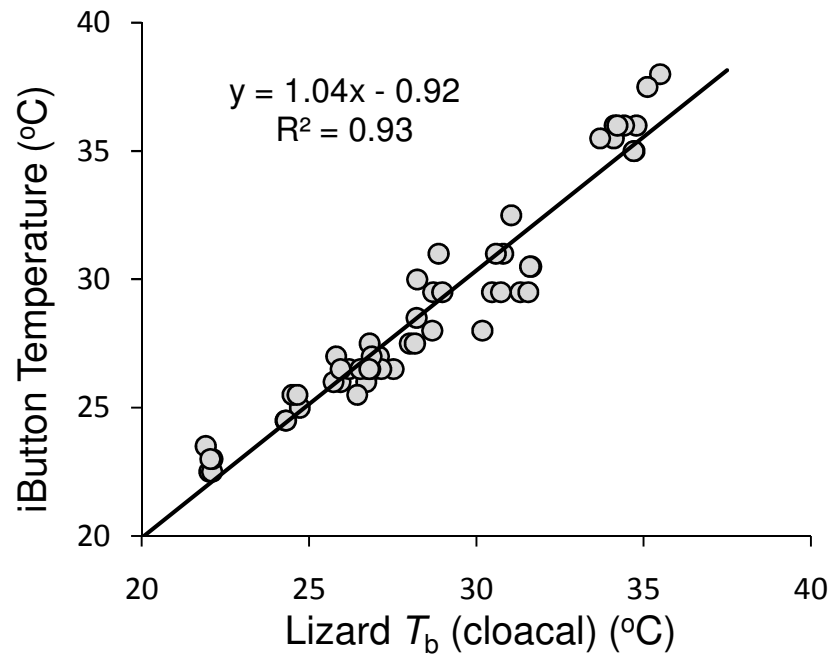
Figure 2.3. A linear regression indicating the correlation between internal body temperatures (T_b-cloacal) and body surface temperatures measured with modified Thermochron iButton data loggers. Individual readings represent equilibrium temperatures recorded beneath a 250 W IR bulb positioned at varying heights (N = three lizards).

2.3.2.3 Preferred temperature range (T_p) estimation

The body temperatures of each lizard were recorded at 10 minute intervals for 14 days, starting the day after capture (i.e. field-fresh). Lizards naturally thermoregulate between an upper and lower temperature threshold (Barber and Crawford 1977). The body temperatures from every instance of active thermoregulation where an upper and lower threshold is evident (therefore not achieved through conformity) were identified graphically, extracted and used for the analysis (Figure 2.4). The preferred temperature range (T_p) for each individual was determined as the central 80 % of selected T_bs (i.e. 10 and 90 percentiles) (Bauwens *et al.* 1995; Gvozdik 2002; Diaz *et al.* 2006) for each experimental day. The central 50 % was also determined in order to provide results comparable to other studies (Hertz *et al.* 1993; Clusella-Trullas *et al.* 2007). The upper and lower limits of both the central

80 % and 50 % of selected temperatures were calculated for each individual for each day. The deviation between these upper and lower limits was regarded as the breadth of T_p, and "breadth"-values were therefore calculated for each individual during each day.
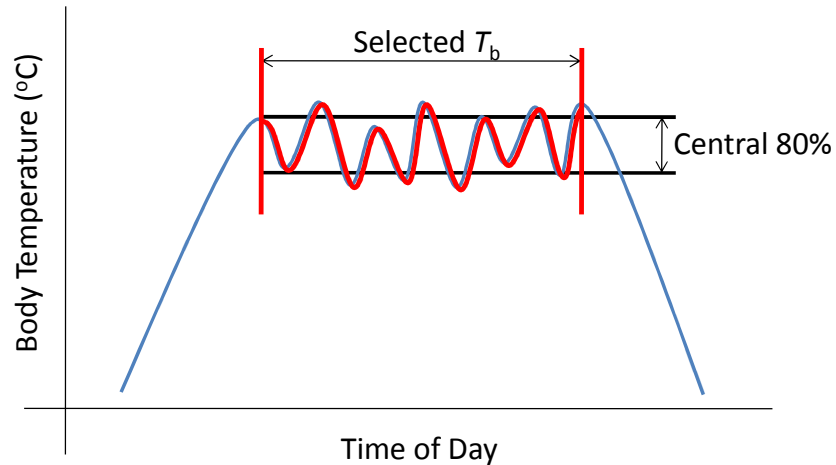
Figure 2.4. Illustrating the technique currently applied to calculate the preferred temperature range (T_p) of *C. cataphractus*. Periods of active thermoregulation were graphically identified, extracted and pooled per individual per day. The central 80% of these selected body temperatures (Bauwens *et al.* 1995) were then calculated for each individual per experimental day. The means of the aforementioned central 80 % selected T_bs were considered as the preferred temperature range (T_p).

2.3.2.4 Lizard Activity

The activity frequencies of lizards were quantified on the basis of the T_bs experienced on each experimental day. In particular, since crevices were positioned in the cool end of each photo-thermal gradient, lizards had to emerge and move towards the opposite end in order to increase T_b. Body temperatures exceeding 25 °C therefore indicate emergence from crevices, movement towards and exploitation the heat-source (since crevice temperature typically equalled 22°C). The activity frequencies were determined for each lizard across the respective experimental days.

2.3.3 Statistical analysis

Normality of data was assessed through Shapiro-Wilk's W-test. Because of the nature of the data (being both repeated measures across days and unbalanced due to missing values)

generalized linear mixed model analyses (PROC MIXED (when residuals were normally distributed) and PROC GLIMMIX (when residuals were not normally distributed), SAS 9.1, SAS Institute Inc., USA) were used with experimental day, season, site and gender as classification variables and experimental day as the repeated measure. Because individuals were randomly chosen from the natural population, subject represents a random factor which cannot form part of the (repeated measures ANOVA) model statement, but was however included as the subject effect in the repeated statement. The compound symmetry (CS) covariance structure was used, based on the Akaike Information Criterion (Littell *et al.* 1996). Subjects were assumed independent among seasons since certain individuals used in autumn could not be retrieved in the field during spring.

The means of preferred temperatures (i.e. the extracted T_bs when lizards were actively thermoregulating (see Figure 2.4)) were recorded for each lizard per experimental day. A generalized linear mixed model (PROC MIXED, SAS inc.) with experimental day, season, site and gender as classification variables and experimental day as the repeated measure was subsequently performed on these (daily) mean preferred temperatures. When preferred temperatures (T_p) were considered across sites and across seasons, values for experimental day one was significantly higher than days three, four, five, seven, eight, nine and 12 (Tukey-Kramer adjusted P: 3, $P = 0.02$; 4, $P = 0.01$; 5, $P = 0.01$; 7, $P < 0.01$; 8, $P < 0.01$; 9, $P < 0.01$; 12, $P = 0.02$). Day one was subsequently removed from all analyses and acted as an acclimation period. The high T_ps on day one were most likely due to amplified activity caused by the stress of handling, transport and introduction to the new unfamiliar laboratory environment.

The upper and lower limits of T_p (i.e. the 10, 90, 25 and 75 percentiles of the extracted T_bs (see Figure 2.4)) were calculated for each individual per experimental day. Moreover, the breadths of T_p (deviation between the upper and lower limit of the central 80 % and 50 % of preferred body temperatures (Figure 2.4)) were calculated for each lizard per experimental day. Both the upper and lower limts of T_p as well as the breadths of T_p were subsequently analysed using a non-parametric generalized linear mixed model (PROC

GLIMMIX, SAS inc.) with experimental day, season, site and gender as classification variables and experimental day as the repeated measure. Temporal autocorrelation of data was assessed with Time Series Analysis (STATISTICA 8, Statsoft Inc., USA). Typically, body temperatures taken 30 minutes apart were independent of each other.

The among-day repeatability (r) of T_p was calculated as the intra-class correlation coefficient (Sokal and Rohlf 1981; Clusella-Trullas *et al.* 2007), applying variance components derived from one-way ANOVAs, as prescribed by Lessells and Boag (1987). Repeatability was calculated from daily mean preferred temperatures selected in photo-thermal gradients by lizards from the coastal and inland population during autumn and spring respectively. The 95 % confidence limits of r were calculated according to Krebs (1999). Body mass had no significant effect on T_p and was subsequently ignored during all further analyses ($P > 0.45$). Lizard activity frequencies (section 2.4.3) were compared among populations and across seasons with two by two tables applying the Chi-square test. All data were analyzed using SAS Enterprize Guide 3 (SAS Institute Inc., USA) and STATISTICA 9 (Statsoft Inc., USA). Means are reported ± standard deviation. Probability values (P) of less than 0.05 were accepted as significant.

2.4 Results

2.4.1 Preferred temperature range (T_p)

Mean preferred temperatures (T_p) did not vary significantly among the inland and coastal populations during autumn and spring (overall: $F_{1,19} = 4.12$; $P = 0.06$; autumn: $P > 0.65$; spring: $P > 0.30$, Tukey-Kramer), nor among seasons within each population (overall: $F_{1,19} = 0.1$; $P = 0.75$; inland: $P > 0.90$; coastal: $P > 0.90$, Tukey-Kramer) (Tables 2.1 and 2.2; Figure 2.4).
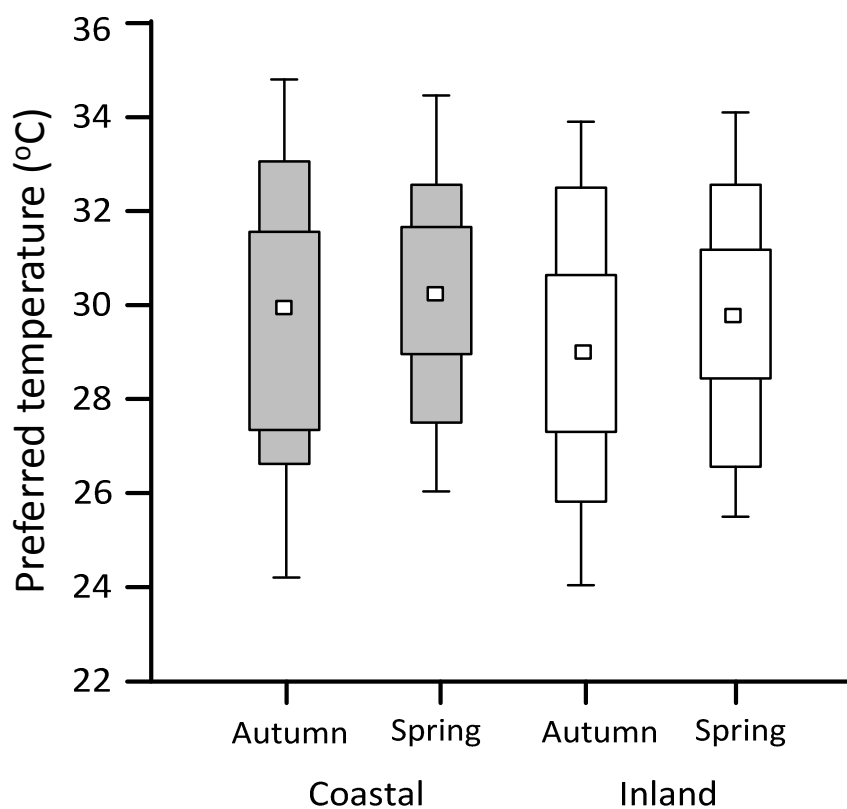
Figure 2.5. Preferred body temperatures (T_p) selected by two populations of *C. cataphractus* (Grey: coastal; Clear: inland) in laboratory thermal gradients during autumn and spring (mean, mean upper and lower limits of the central 50 % and 80 % preferred temperatures (vertical rectangles), ± 2SD (whiskers)). Body temperatures were recorded across 13 consecutive days ($N = 2506$ measurements).

Table 2.1. The preferred body temperatures (T_p, °C) of a coastal and inland population of *Cordylus cataphractus* estimated during autumn and spring. Body temperatures of 24 subject units (N) were recorded in a laboratory thermal gradient (T_e: 22 °C – 55 °C) at 10 minute intervals for 13 days.

Population	Season	N	Mean	Percentiles				SD	Var	SE
				25 [a]	75 [a]	10 [b]	90 [b]			
Coastal	Autumn	5	29.5	27.3	31.6	26.3	33.0	2.6	6.9	0.19
	Spring	7	30.2	28.9	31.7	27.5	32.6	2.1	4.4	0.07
	Overall	12	30.1	28.7	31.7	27.3	33.0	2.2	4.9	0.06
Inland	Autumn	6	29.0	27.3	30.6	25.8	32.5	2.5	6.2	0.13
	Spring	6	29.8	28.4	31.2	26.6	32.6	2.2	4.6	0.07
	Overall	12	29.6	28.0	31.2	26.3	32.6	2.3	5.2	0.06
Grand Mean		24	29.8	28.4	31.2	26.8	32.6	2.3	5.1	0.05

[a] The lower and upper bounds of the central 80 % of observed T_bs (Bauwens *et al*. 1995).
[b] The lower and upper bounds of the central 50 % of observed T_bs (Hertz *et al*. 1993).

Gender had no significant effect on mean T_P (Table 2.2); in fact, of the potential sources of variation on mean T_P explored, only experimental day and the season-day interaction was found to be significant (Table 2.2). The T_ps of the two populations were subsequently re-analyzed per season through repeated measures ANOVA with (experimental) day and gender as classification factors and day as repeated measure. Day was a significant source of variation in mean T_p during spring in both the coastal ($F_{12,38} = 2.06$; $P = 0.05$) and inland ($F_{12,30} = 2.88$; $P < 0.01$) populations, but not during autumn. Least squares post hoc analyses for spring further indicated that mean T_p varied significantly between day 12 and days five ($P < 0.01$), seven ($P = 0.03$) and 14 ($P = 0.05$) in the coastal population, whereas day six varied significantly from days 10 ($P = 0.03$) and 12 ($P < 0.01$) in the inland population (Tukey-Kramer adjusted P's).

Table 2.2. Generalized linear mixed model analysis (PROC MIXED repeated measures) of the preferred body temperatures recorded for a coastal and inland population of *C. cataphractus* during autumn and spring. The analysis was performed on daily means for each individual across the 13 day experimental period (N = 209 daily means, N = 24 subject units, male-female ratio 11:13).

Source of variation	*df*	*F*	*P*
Day	12,137	2.3	0.01*
Season	1,19	0.1	0.75
Population	1,19	4.12	0.06
Gender	1,19	0.72	0.41
Season*Day	12,137	2.02	0.03*
Population*Day	12,137	1.09	0.37
Season*Population	1,19	0.09	0.77
Season*Population*Day	12,137	1.53	0.12

Table 2.3. Generalized linear mixed model analyses (PROC GLIMMIX repeated measures) of the upper and lower limits of the central 80 % and 50 % of preferred temperatures selected by a coastal and inland population of *C. cataphractus* in laboratory thermal gradients during autumn and spring (N = 24 subject units, male-female ratio 11:13). The upper and lower limits of both the central 80 % and 50 % selected temperatures were calculated for each individual per experimental day.

Source of variation	*df*	Lower limit 80 *F*	Lower limit 80 *P*	Upper limit 80 *F*	Upper limit 80 *P*	Lower limit 50 *F*	Lower limit 50 *P*	Upper limit 50 *F*	Upper limit 50 *P*
Day	13,151	0.82	0.64	4.20	<0.01*	2.12	0.02*	3.93	<0.01*
Season	1,9	3.45	0.08	0.05	0.82	2.87	0.11	0.03	0.87
Population	1,9	2.92	0.10	4.38	0.05*	2.60	0.12	4.76	0.04*
Gender	1,9	1.87	0.19	0.39	0.54	1.07	0.31	0.24	0.63
Season*Population	1,9	3.01	0.10	0.29	0.60	2.71	0.12	0.78	0.39
Season*Day	13,151	0.44	0.95	2.85	<0.01*	0.55	0.89	2.85	<0.01*
Population*Day	13,151	1.11	0.35	1.27	0.24	1.39	0.17	2.20	0.01*
Season*Population*Day	13,151	0.70	0.76	0.64	0.82	1.24	0.26	1.30	0.22

Experimental day had a significant effect on the upper limit of the central 80 % preferred body temperatures (T_p) (Bauwens *et al.* 1995), as well as the upper and lower limits of the central 50 % T_ps (Hertz *et al.* 1993) (Table 2.3). The season-day interaction had a significant effect on the upper limits of both the central 80 % and 50 % T_ps (Table 2.3). Furthermore, the population-day interaction had a significant effect on the upper limit of the central 50 % T_ps (Table 2.3). The upper and lower limits of T_p in the two populations were subsequently re-analyzed per season through repeated measures ANOVA with day and gender as classification factors, and day as repeated measure. Experimental day was a significant source of variation in the lower limit of the central 50 % preferred body temperatures ($F_{12,42}$ = 2.28; P = 0.02) and upper limits of the central 80 % ($F_{12,42}$ = 1.96; P = 0.05) and 50 % T_ps ($F_{12,42}$ = 2.35, P = 0.02) in the inland population during spring, but not in autumn neither in the coastal population during both seasons. Least squares post hoc analyses however indicate no significant among-day variation in the lower limit of the central 50 % T_ps, whereas the upper limit of the central 80 % selected T_ps varied significantly only among days six and 12 (P = 0.05), and the upper limit of the central 50 % selected T_ps varied significantly only among days two and 12 (P = 0.05) (Tukey-Kramer adjusted P's).

The upper limits of both the central 80 % and 50 % preferred body temperatures varied significantly among populations (Table 2.3). A least squares post hoc analysis however indicated no significant pair-wise differences in the 80 % and 50 % upper limits of T_p among populations during the respective seasons (P < 0.1, Tukey-Kramer). The breadths of the central 80 % and 50 % of preferred body temperatures did not vary significantly among populations or across seasons (Table 2.4).

Table 2.4. Generalized linear mixed model analyses (PROC GLIMMIX repeated measures) of the breadths of the respective central 80 % and 50 % of preferred body temperatures selected by a coastal and inland population of *C. cataphractus* in laboratory thermal gradients during autumn and spring (N = 24 subject units, male-female ratio 11:13). The breaths of T_p (i.e. the difference between the upper and lower limits of T_p (i.e. 10, 90 and 25, 75 percentiles)) were calculated for each individual per experimental day.

Source of variation	df	Breadth 80		Breadth 50	
		F	P	F	P
Day	12,137	1.10	0.36	1.47	0.14
Season	1,19	1.18	0.29	4.00	0.06
Population	1,19	2.12	0.16	2.73	0.11
Gender	1,19	0.07	0.79	0.34	0.57
Season*Population	1,19	2.07	0.17	1.88	0.19
Season*Day	12,137	1.64	0.09	1.76	0.06
Population*Day	12,137	0.50	0.91	0.74	0.71
Season*Population*Day	12,137	0.41	0.96	1.66	0.08

Table 2.5. Among-day repeatability (described by the intraclass correlation coefficient (r) (Lessells and Boag 1987)) of the mean preferred body temperatures (T_p) of a coastal and inland population of *Cordylus cataphractus*, estimated during autumn and spring. The analysis was performed on daily mean T_ps calculated from the body temperatures recorded in a laboratory thermal gradient (T_e: 22 °C – 55 °C) at 10 minute intervals for 13 days. The 95 % lower and upper confidence intervals (LCL, UCL) were calculated as prescribed by Krebs (1999). The degrees of freedom, F and P-values describe the among-subject (lizard) variation present in T_p (one-way ANOVA).

Population	Season	N	ANOVA			Repeatability (r)	LCL	UCL
			df	F	P			
Coastal	Autumn	5	4,26	2.79	0.05*	0.24	0.07	0.44
	Spring	7	6,62	5.90	<0.01*	0.33	0.17	0.51
Inland	Autumn	6	5,43	7.35	<0.01*	0.44	0.26	0.62
	Spring	6	5,54	14.98	<0.01*	0.63	0.45	0.77

2.4.2 Repeatability

There was significant variation in mean T_p among individuals at the coastal and inland populations during both summer and autumn (Table 2.5). The among-day repeatability (r) of mean T_p ranged from 0.24 to 0.63, being consistently lower at the coastal than inland population in autumn and spring (Table 2.5). Moreover, among-day r was lower in autumn than spring at both the coastal and inland populations (Table 2.5).

2.4.3 Lizard activity

The frequency of daily instances when lizards moved to the heated sections of photo-thermal gradients was significantly lower during autumn than spring in lizards from both the coastal (Chi-square value (χ^2) = 13.04, $P < 0.01$) and inland populations (χ^2 = 3.68, $P = 0.05$) (Figure 2.5). Conversely, activity did not vary significantly among populations during both autumn ($\chi^2 = 3.29$, $P = 0.07$) and spring ($\chi^2 = 0.03$, $P = 0.87$) (Figure 2.6).
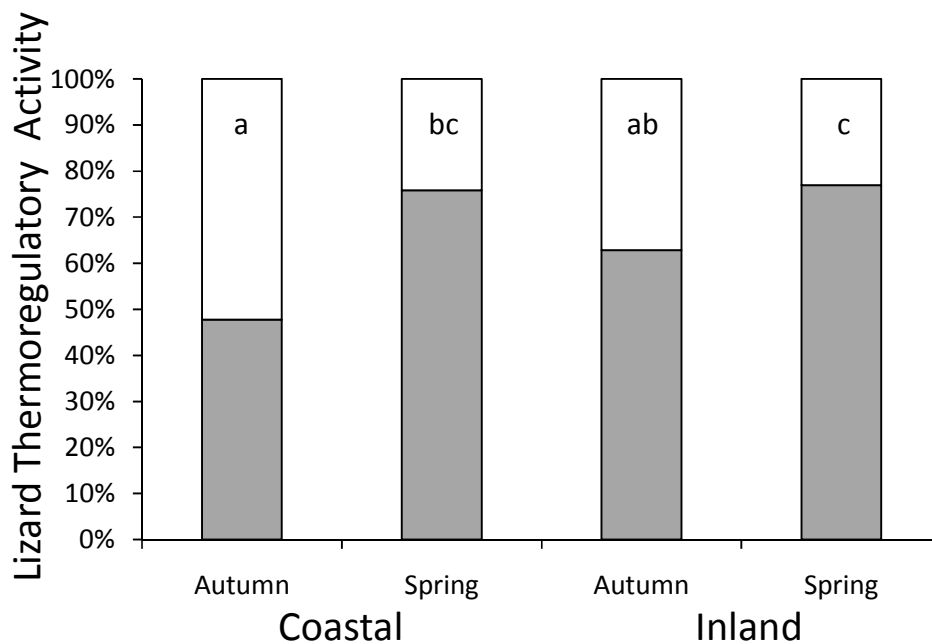

Figure 2.6. The patterns of active exploitation of heat sources in laboratory thermal gradients (and therefore emergence from crevices) of members of a coastal and an inland *C. cataphractus* population during autumn and spring (grey-scale: exploitation of heat source; clear: no exploitation of heat source).

2.5 Discussion

The preferred temperature range (T_p), defined as the predicted range of body temperatures within which an ectotherm functions optimally and therefore strives to attain, is recognized as an important component of quantitative indices of thermoregulation (for example the T_b-T_p and T_b-T_e differentials in the field (Hertz *et al.* 1993)). Although T_p has been estimated in numerous lizard species (Huey 1982; Angilletta *et al.* 2002), seasonal and geographical variation in this biological parameter is less well documented (e.g. Christian and Bedford 1995; Angilletta 2001; Diaz *et al.* 2006; Du 2006).

The aim of the current study was to describe the preferred temperature range of *C. cataphractus* and to investigate temporal and spatial plasticity therein. The estimated T_ps represent both, respectively and collectively, (as an overall mean for the species) the lowest recorded among cordylids to date (grand mean T_p: 29.8 ^{o}C ± 2.3 ^{o}C; mean T_p range: 26.8 ^{o}C to 32.6 ^{o}C (central 80 % selected T_bs, Bauwens *et al.* 1995)). The observed mean T_p corresponds closely to an earlier estimate provided by Truter (2007) for an inland *C. cataphractus* population (Lamberts Bay district, South Africa) during spring (i.e. 30.1 ^{o}C). The current mean T_p of both the coastal and inland *C. cataphractus* populations did not vary significantly among seasons, neither did mean T_p vary significantly among populations within each season.

Although T_p is generally variable among reptile genera (Angilletta and Werner 1998), T_p tends to be conserved among related species (Licht *et al.* 1966; Huey 1982; Angilletta and Werner 1998; Kohlsdorf and Navas 2006). Thermal preference was found to be relatively variable within the Cordylidae family with a maximum among-species difference of 4.4 ^{o}C (Table 2.6). The low T_p observed for *C. cataphractus* in comparison to other cordylids may be related to the group-living life strategy, supported by the fact that *C. cataphractus* is the only group-living cordylid for which T_p has been estimated.

Table 2.6. The mean preferred body temperatures (T_p) (± 1SD) reported for members of the Cordylidae family.

Species	Season	T_p	Reference
Cordylus cataphractus	Autumn	29.2 ± 2.5	Current study
	Spring	30.0 ± 2.1	Current study
Pseudocordylus capensis	Spring	30.4 ± 1.3	Janse van Rensburg 2009
Pseudocordylus melanotus m.	Summer	31.0 ± 0.1*	McConnachie *et al.* 2009
	Winter	30.1 ± 0.1*	McConnachie *et al.* 2009
Platysaurus intermedius w.	Summer	31.5 ± 1.7	Lailvaux *et al.* 2003
Cordylus cordylus	Summer	32.1 ± 0.7	Clusella-Trullas *et al.* 2007
Cordylus vittifer	Laboratory acclimated	32.1 ± 1.8	Skinner 1991
Cordylus niger	Summer	32.6 ± 0.3	Clusella-Trullas *et al.* 2007
Cordylus jonesi	Laboratory acclimated	33.5 ± 0.3	Wheeler 1986
Cordylus polyzonus	Summer	33.6 ± 0.3	Clusella-Trullas *et al.* 2007
Cordylus oelofseni	Summer	33.6 ± 0.3	Clusella-Trullas *et al.* 2007

*± standard error

The solitary-living *Cordylus polyzonus* share habitats with *C. cataphractus* (Visagie 2001), and in certain cases even crevices (personal observation). Unlike *C. cataphractus*, *C. polyzonus* remains fully active during the dry season (Visagie 2001), and further maintains a seven times higher resting metabolic rate (Mouton *et al.* 2000b), and fat bodies three times smaller than *C. cataphractus* have been recorded (Flemming and Mouton 2002). The contrast between *C. cataphractus* and *C. polyzonus* in relation to seasonal activity, RMR and fat bodies is likely a function of their alternate life strategies (i.e. group-living versus solitary-living) and the subsequent effects on energy budgets, supported by the fact that RMR and the fat bodies of *C. polyzonus* correspond relatively to that observed in other solitary-living cordylids (Mouton *et al.* 2000a; Mouton *et al.* 2000b; Visagie 2001; Flemming and Mouton 2002; Hayward 2008). The fact that T_p was 3.8°C lower in *C. cataphractus* than reported for *C. polyzonus* (Clusella-Trullas *et al.* 2009) suggests that T_p is also related to the life strategy employed (i.e. grouping versus solitary). However, since no detailed field thermoregulation study has been conducted on *C. polyzonus*, further study, employing quantitative indices such as the Hertz *et al.* (1993) approach is needed. Similarly, the T_ps and thermal ecology of other permanently aggregating cordylids (i.e. *Cordylus macropholis*, *Cordylus peersi*,

Platysaurus broadleyi (Mouton 2011)) are unknown and such data may aid interpreting the relatively low T_p observed in *C. cataphractus*.

Experimental day (describing among-day variance) was a significant source of variation in the mean T_p, lower limit of the central 50 % preferred body temperatures, as well as the upper limits of the central 80 % and 50 % T_ps, indicating significant variation in the T_bs selected in photo-thermal gradients across the 13 day experimental period. When the populations were analysed separately per season, experimental day had a significant effect on mean T_p in both populations, but only during spring, as well as on the lower limit of the central 50 % T_ps and upper limits of the central 80 % and 50 % T_ps, yet only in the inland population and only during spring.

The methodology applied (i.e. laboratory thermal gradient) and acclimation represent two possible sources of variable T_ps across days (Clusella-Trullas *et al.* 2007). The fact that experimental day only had a significant effect on mean T_p during spring, furthermore being localized to day six in the coastal and day 12 at the inland population, suggests that the experimental setup or acclimation was not the source of among-day variation in T_p since exposure conditions were kept constant among trials.

Other factors such as seasonal behaviour patterns may have affected the T_b selection across days (Huey 1982). At least two lizards captured from the same social group were housed together per thermal gradient. The spring trials occurred during peak mating season (Flemming and Mouton 2002), and mating and courtship or other social behaviour may therefore have altered thermoregulatory activity, resulting in the significant variation in T_p across days. Further investigation (e.g. behavioural observations) is however needed to assess social behaviour as source of variance in T_p.

Reptiles are known to express irregular activity patterns, and remain inactive for a day or longer, even though food is available and climatic conditions are favourable (Nagy 1973; Bradshaw *et al.* 1980; Huey 1982; Brown and Shine 2002; Kerr *et al.* 2008). The observed among-day variation may therefore simply be the result of natural behavioural plasticity (Kerr *et al.* 2008).

The majority of researchers base T_p estimates on one- (Patterson and Davies 1978; Lailvaux *et al.* 2003) or two-day laboratory trials (Angilletta *et al.* 1999; Gvozdik and Castilla 2001; Catenazzi *et al.* 2005; Yang *et al.* 2008; McConnachie *et al.* 2009). However, the significant effect of experimental day on T_p as currently observed suggests that T_p estimates based on longer laboratory trials will provide more realistic estimates of thermal preference.

Repeatability describes the inter-individual variance in proportion to intra-individual variance in a particular characteristic such as thermal preference (Lessells and Boag 1987; Boake 1989). The among-day repeatability (r) of mean T_p observed for *C. cataphractus* was variable among populations and across seasons ranging from 0.24 to 0.63. The variable among-day r indicates that the extent of inter-individual variance across days was inconsistent among populations and across seasons (Lessells and Boag 1987). The among-day r's reported for the coastal population during autumn and spring, as well as the inland population in autumn was low and corresponds relatively to among-day r-values reported by Clusella-Trullas *et al.* (2007) for four other cordylids, whereas the among-day r reported for *C. cataphractus* in the present study for the inland population during spring is the highest reported among cordylids to date. The lower among-day repeatability in T_p observed in both populations during autumn indicates that the variance originating from inter-individual differences was low in proportion to the variance originating from intra-individual differences (Lessells and Boag 1987). *Cordylus cataphractus* is known to exhibit repressed activity during autumn (Visagie 2001), which may have contributed to the low among-day repeatability observed at the time.

Repeatability is often used in the literature as a yardstick to describe genetic variation in a specific trait (e.g. T_p), under the assumption that differential expression (among individuals) represents real genetic variation (Boake 1989; Clusella-Trullas *et al.* 2007; English *et al.* 2010). Clusella-Trullas *et al.* (2007) calculated among-day repeatability (r) of T_p in four cordylids under three acclimation states (i.e. field-fresh, nine day acclimated and 12 day acclimated) and reported variable r's within species (varying by up to 0.48), but with no definite trend in relation to acclimation state (e.g. field fresh higher). The only other report of

repeatability in lizard T_p is given by Le Galliard *et al*. (2003) who reported a *r* of 0.66 for *Lacerta vivipara* on measurements taken across two days. The fact that the among-day repeatability was generally low and variable in both the current study and Clusella-Trullas *et al*. (2007) suggests that among-day repeatability does not implicitly reflect genetic variation in T_p.

The legitimacy of the methodology for T_p determination (i.e. thermal gradients) has been questioned, primarily due to the assumption that ecological and physiological costs are absent in laboratory enclosures (Christian and Weavers 1996; Currin and Alexander 1999). The protocol for T_p determination followed in the current study was specifically designed to mimic natural conditions, minimize human contact and facilitate natural (behavioural) thermoregulation. If the methodology for determining T_p was effective in translating the physiological target of thermoregulation, one would have expected at least a degree of consistency (invariable) in among-day repeatability of T_p among populations and across seasons, which was not the case in the current study. The direct estimation of neurological set-points has been suggested as an alternative to T_p estimated in laboratory thermal gradients (Currin and Alexander 1999). A comparison between the *r*'s of laboratory estimated T_ps and neurological upper and lower set-point temperatures, and the seasonal and geographical variation thereof may provide further information on the reliability and applicability (in ecological studies) of these respective parameters.

Wills and Buepre (2000) employed a randomization approach to determine whether timber rattlesnakes thermoregulate actively in nature. The randomization technique does not rely on a preferred temperature range (T_p), but instead compares the potential (randomized) distributions of T_e and T_b (10 000 iterations). Such an approach in light of the low repeatability observed in T_p may be a useful alternative to the use of T_p to assess thermoregulation in reptiles (Wills and Buepre 2000). The exact *P*-values (displaying significance) determined in the randomization approach is however directly dependent on sample sizes and the number of randomization trials and is therefore not of use in seasonal or population-wide assessments of thermoregulation, but simply provides an indication

whether animals are likely thermoregulating actively and/or whether they are impaired by thermal constraints (Wills and Buepre 2000).

Even though reptile populations (of the same species) may inhabit diverse thermal habitats (e.g. altitudinal gradients), reports of population-level variation in reptile thermal preference are limited in the litterature (Du 2006). In contrast, conservatism in T_p among populations have been observed by various researchers (e.g. Van Damme *et al.* 1989; Brown 1996; Gvozdik and Castilla 2001; Gvozdik 2002). The lack of significant variation in T_p (i.e. mean, upper and lower limits of the central 80 % and 50 % preferred body temperatures) among the coastal and inland *C. cataphractus* populations during autumn and spring therefore corresponds to the general trend of T_p conservatism in reptiles (Van Damme *et al.* 1989; Brown 1996; Gvozdik and Castilla 2001; Gvozdik 2002).

Unlike geographical variation, seasonal variation in T_p is a common phenomenon in reptiles (Patterson and Davies 1978; Van Damme *et al.* 1986; Firth and Belan 1998; Diaz *et al.* 2006; McConnachie *et al.* 2009), being accomplished through thermal acclimatization (i.e. reversible phenotypic plasticity) (Seebacher 2005). Seasonal shifts in T_p generally occur in the direction of the prevalent operative environmental temperatures (T_e) (Van Damme *et al.* 1986; Diaz and Cabezas-Diaz 2004; McConnachie *et al.* 2009), hence reducing costs associated with thermoregulation (Huey and Slatkin 1976). In fact, reports of conservative (invariable) T_ps across seasons in response to definite (seasonal) variation in the available environmental temperatures (i.e. T_e) are rare in reptiles (Van Damme *et al.* 1987; Schauble and Grigg 1998; Sepúlveda *et al.* 2008).

In the current study, thermal preference was estimated during the respective annual peaks in food abundance and scarcity, partly to test whether the annual energy crisis (associated with group-living behaviour) (Mouton *et al.* 2000a; Hayward 2008) influences T_p. Certain reptiles can employ acclimatization to lower T_p during periods of food scarcity, hence lowering metabolic energy expenditure and water flux (Christian and Bedford 1995; Christian and Bedford 1996; Haynie 2001). For instance, Christian and Bedford (1995) reported a significant seasonal decrease in T_p from the cooler-wet to warmer-dry season in

Chlamydosaurus kingii. Christian and Bedford (1995) suggested the altered T_p as an active mechanism to lower metabolic expenditure and water flux, which is supported by the fact that *C. kingii* maintains dramatically decreased field metabolic rates during the dry season (Christian and Green 1994). Since *C. cataphractus* is known to suffer severe (food) resource limitation during autumn (Mouton *et al.* 2000a; Flemming and Mouton 2002) the prevalence of altered T_p (such as described for *C. kingii*) through acclimatization is expected (Wilson and Franklin 2002; Seebacher 2005). *Cordylus cataphractus* however exhibits a degree of thermally independent metabolism and highly repressed resting metabolic rate (RMR) (0.05 ml O_2 ml.g^{-1}.h^{-1} at 30°C), 68 % lower than that observed in any other cordylid to date (Mouton *et al.* 2000b). The exceptionally low RMR suggests that lowered T_p will not necessarily benefit the species in relation to metabolic expenditure. Surprisingly the RMR reported by Mouton *et al.* (2000b) was determined during October (within peak activity season) when *C. cataphractus*'s metabolic requirements are high, since fat bodies are predominantly deposited at that time the of year (Flemming and Mouton 2002). Nonetheless, although T_p did not vary significantly among seasons in *C. cataphractus*, the variation followed a consistent pattern, on average being 0.4 °C and 0.6 °C lower during the warmer dry autumn at the coastal and inland populations respectively (see Figure 2.5). Dismissing the possibility that a low T_p may function as countermeasure to food scarcity (because of the absence of significant seasonal variation) is therefore premature.

The modified iButton temperature loggers proved to be a worthy substitute for the conventional grab-and-jab or trailing thermocouple approaches to T_b measurement in laboratory trials for the following reasons: T_b-iButton correspond relatively closely to internal body temperatures (Shine *et al.* 2003; Figure 2.3); modified iButtons are relatively cost effective and easy to construct (Robert and Thompson 2003; Lovegrove 2009); human contact to animals can be kept at a minimum; and T_bs can be recorded continuously for prolonged periods.

Each body temperature measurement taken in the current study was validated through a correlation function (of iButton temperature versus internal body temperature)

obtained by expressing three iButton-carrying individuals to a range of equilibrium temperatures (Figure 2.3). A more accurate approach would however have been to calibrate iButtons independently (i.e. generate a correlation function) for each lizard used in the study, since relationship between internal and iButton T_b is expected to vary slightly among individuals.

The projected activity frequency was based on T_bs recorded during the 13 day exposure period, and in reality describes active exploitation of a thermal heat source (i.e. behavioural thermoregulation), rather than implicit activity. The frequency of instances (i.e. days) when lizards did not exploit the provided heat-source was significantly higher during autumn than spring in both populations (Figure 2.6).

As mentioned earlier, autumn is the proposed period of repressed activity in *C. cataphractus*, when lizards predominantly remain within crevices and occasionally move up to 0.10 m from crevices (Visagie 2001). The lowered activity of *C. cataphractus* has been ascribed to energetic constraints amplified by their group-living life strategy (Visagie 2001; Hayward 2008). The question whether individuals are dormant (i.e. aestivating) or fully active whilst in retreat has however not been empirically tested. The current results suggest that lizards are indeed active and will emerge from crevices for thermoregulatory purposes, although not necessarily at a daily frequency and that activity is lowered, yet not absent. Moreover, the current results suggest that lizard may actively regulate body temperatures inside crevices during autumn when *C. cataphractus* known to rarely emerge (Visagie 2001).

2.6 Conclusion

The current results indicate that *C. cataphractus* exhibits a low preferred temperature range (26.8 $^{\circ}$C to 32.6 $^{\circ}$C; overall mean T_p of 29.8 $^{\circ}$C) the lowest reported among cordylids to date. The low T_p may be associated with the group-living life strategy of *C. cataphractus* (and more specifically the associated amplified food constraints); a prediction supported by the fact that the mean T_p was 3.2 $^{\circ}$C lower than that of the solitary-living *C. polyzonus* which in many cases share habitats with *C. cataphractus*. An exploration of thermal preference in other permanently aggregating cordylid species may aid in identifying the source of the low T_p observed in *C. cataphractus*. The laboratory trials were performed across 13 days, and experimental day was a significant source of variance in mean T_p, the upper limits of the central 50 % and 80 % T_ps as well as the lower limit of the central 50 % T_ps. Although the exact cause of the observed variation in T_p across days remains unclear, social interactions or natural behavioural plasticity represent likely sources of T_p variability across days. The among-day repeatability of T_p was variable among populations and across seasons suggesting that the methodology for determining T_p does not implicitly describe the physiological target T_b range. Thermal preference was conservative at both seasonal and geographical scale, yet being slightly lower during the warmer dry autumn period. Seasonal acclimatization may function to increase energy efficiency by either decreasing thermoregulatory costs (i.e. shifting T_p towards the prevalent T_e), or by lowering T_p irrespective of environmental temperatures in order to lower metabolic expenditure and water flux (Christian and Bedford 1995). Although T_p did not vary significantly at seasonal scale, the lower T_p during the dry autumn suggest that acclimatization targeted at resource (food and water) preservation may be at play. Finally, the current results indicate *that C. cataphractus* performs active behavioural thermoregulation (in the laboratory) during autumn when the field activity of the species is known to be repressed. The proportion of days when lizards emerged from crevices and exploited the thermal opportunities provided was however significantly lower during autumn than spring in both populations.

Chapter 3

Seasonal variation in the thermal habitat and consequent thermoregulatory patterns of the group-living lizard, *Cordylus cataphractus*

3.1 Abstract

Because of ectothermy, thermal ecology is essential to consider when interpreting the physiology, behaviour and life strategies of reptiles. *Cordylus cataphractus* is an uncharacteristic member of the family Cordylidae due to a permanent group-living life strategy, exceptionally low resting metabolic rate, enlarged fat bodies, lowered seasonal surface activity and heavy dermal armature. Although *C. cataphractus* is generally well studied, little is known regarding the field thermal ecology of the species. The repressed surface activity reported for *C. cataphractus* occurs during summer, autumn and winter. While food constraints associated with their group-living life strategy in a semi-arid context has been implicated as the determining factor for lowered activity, the affect of seasonal trends in the thermal habitat on activity has not been investigated. The quality of the thermal habitat and thermoregulatory strategy/patterns of *C. cataphractus* was explored in a coastal population during summer, autumn, winter and spring. The study was conducted in relation to four main indices namely: thermal habitat quality; accuracy of thermoregulation; effectiveness of thermoregulation and thermal exploitation. These indices were derived from environmental operative temperatures (T_e) (measured with copper lizard models) and field body temperatures (T_b) (measured with modified Thermochron iButton temperature loggers), in combination with the preferred temperature range (T_p) known for *C. cataphractus*. Thermal habitat quality varied seasonally being most favourable during autumn followed by summer, spring and winter respectively. At micro-spatial scale, operative environmental temperatures (T_e) and the subsequent thermal habitat quality varied significantly around rocks among aspects (NESW) during all four seasons. This variation provides an incentive

for intra-group male-male competition since *C. cataphractus* males are highly territorial. Similar to other cordylids studied to date, *Cordylus cataphractus* performed active (behavioural) thermoregulation and the extent thereof varied seasonally as a function of thermal habitat quality. The seasonal surface activity patterns reported for *C. cataphractus* correspond to the general micro-spatial distribution of thermally favourable microsites during autumn and spring. Although the lowered surface activity observed in *C. cataphractus* may therefore be linked to temperature, temperature in combination with food availability and other factors such as predation risk and feeding behaviour seems a more likely explanation. The current mean T_bs for summer, when compared to the micro spatial distribution of T_e, suggest that individuals emerged from crevices at the time, unlike earlier reports present in the litterature for the species. Three exceptionally warm days were observed during the summer field trial with T_es of up to 63.6 ^{o}C and lizard body temperatures of up to 40.2 ^{o}C (7.6 ^{o}C higher than the upper bound of the preferred temperature range of *C. cataphractus*) were recorded. The T_e distribution during hot summer days indicated that lizards potentially reached high body temperatures involuntarily whilst being within crevices. Overheating is therefore a real risk even within crevices, especially for groups occurring beneath small rocks.

Key words: Lizard, *Cordylus cataphractus*, thermal ecology, seasonal variation, activity, thermal habitat.

3.2 Introduction

In most reptiles, the majority of physiological processes occur at an optimal level within a narrow range of body temperatures (Peterson *et al.* 1993; Angilletta *et al.* 2002) known as the preferred temperature range (T_p) (Licht *et al.* 1966; Stevenson *et al.* 1985; Bauwens *et al.* 1996; Angilletta *et al.* 1999; Clusella-Trullas *et al.* 2007). Variable and unfavourable thermal habitats may affect T_b, resulting in compromised physiological functioning (Huey 1982; Stevenson *et al.* 1985). Thermoregulation is an active process which, by means of behavioural and physiological modifications (Cowles and Bogert 1944; Bartholomew 1982; Huey 1982; Stevenson 1985; Bauwens *et al.* 1996; Diaz and Cabezas-Diaz 2004; Seebacher and Franklin 2005), counteracts variable/unfavourable environmental temperatures, hence allowing the maintenance of relatively constant T_b, approaching T_p (Huey 1982; Hertz *et al.* 1993). The exploration of thermal habitats and the subsequent thermoregulatory patterns are essential components in the study of reptilian biology, particularly because of the direct relationship between body temperatures and fitness (through physiological temperature dependency) (Huey 1982; Van Damme *et al.* 1991; Angilletta *et al.* 2002; Angilletta *et al.* 2002; Angilletta 2009).

Operative environmental temperatures (T_e) describe the potential (available) field body temperatures (T_b) in a habitat and can be measured with physical/inanimate copper models (with minimum resistance to heat flow) that correspond to a particular organism in relation to size, shape and coloration, therefore integrating the major biophysical pathways of heat transfer (Bakken and Gates 1975; Bakken 1992). In order to quantify the success and extent of thermoregulation performed, a null-model is needed (Hertz *et al.* 1993; Diaz 1997). Operative environmental temperatures (T_e) represent such a model, describing T_b in the absence of thermoregulation (i.e. thermoconformation) (Bakken 1992; Hertz *et al.* 1993; Diaz and Cabezas-Diaz 2004; Row and Blouin-Demers 2006). The degree to which T_e deviates from T_p provides a quantitative estimate of thermoregulatory requirements to reach T_p (i.e. thermal habitat quality, d_e) in a particular habitat (Hertz *et al.* 1993). The thermal habitat of an organism can therefore be mapped in relation to quality (i.e. departure of T_e from T_p) by

placing T_e-models throughout microclimates that are known to be utilized (Huey *et al.* 1989; Kearney 2002).

The thermal characteristics of rocks (and subsequent T_es) vary naturally at micro-spatial scale as a function of diel and seasonal solar cycles (Huey *et al.* 1989; Webb and Shine 1998; Kearney 2002). Temporal and spatial variation in T_e may have pronounced effects on thermoregulatory requirements (within a particular time-frame) and the subsequent time and energy budgets of thermoregulating reptiles (Huey and Slatkin 1976; Blouin-Demers and Weatherhead 2002; Gvozdik 2002). In fact, Magnuson *et al.* (1979) described thermal habitat quality as a resource comparable to food and mates and therefore an entity to compete for, as has indeed been documented in certain reptiles (Huey 1982; Seebacher and Grigg 2001).

Cordylus cataphractus is a member of the family Cordylidae, exhibiting various characteristics atypical for the family such as permanent group-living (Mouton *et al.* 1999), a highly repressed resting metabolic rate (RMR) (Mouton *et al.* 2000b), enlarged fat bodies, low reproductive output (i.e. one sibling per annum) (Flemming and Mouton 2002) and repressed annual activity (Visagie 2001). Although *C. cataphractus* is relatively well studied (e.g. Bauwens *et al.* 1999; Mouton *et al.* 1999; Mouton *et al.* 2000a; Mouton *et al.* 2000b; Flemming and Mouton 2002; Curtin *et al.* 2005; Visagie *et al.* 2005; Costandius *et al.* 2006; Effenberger and Mouton 2007; Shuttleworth *et al.* 2008), the field thermal ecology of this species has not been described, and field thermal ecology studies are limited for the Cordylidae family in general (Stebbins 1961; Bowker 1984; Bauwens *et al.* 1999; Lailvaux *et al.* 2003; Clusella-Trullas *et al.* 2009; McConnachie *et al.* 2009).

The detailed surface activity patterns of *C. cataphractus* is known only for spring, and although individuals may at times visit termite ports meters away from rocks, the vast majority of time is spent in the close proximity of crevices (Effenberger and Mouton 2007). The general site specificity of *C. cataphractus* is likely the result of the combination of a sit-and-wait foraging mode (Mouton *et al.* 2000a), heavy dermal armature and the reliance on crevices as primary defence mechanism (Losos *et al.* 2002). Males are highly territorial, and

typically occupy neighbouring territories of approximately ~0.79 m^2 (Effenberger and Mouton 2007). Micro-spatial variation in the thermal habitat may therefore have a substantial effect on activity patterns and selection/competition for basking sites reflecting on time and energy budgets of individuals (especially males) depending on where they are positioned around rocks and consequently constitute a potential incentive for intra-group competition for thermal habitat quality around rocks.

Although resource availability (i.e. food and water) may be a driving force to be active (Pyke *et al.* 1977; Vitt and Caldwell 2009), in ectotherms, the quality of the thermal habitat may set the temporal (at diel and seasonal scale) and spatial limits for surface activity (Grant and Dunham 1988; Adolph and Porter 1993; Davis and DeNardo 2009). The direct influence of temperature on ectotherm activity is evident in the typical bimodal activity patterns exhibited by many reptiles during hot periods (avoiding risk of overheating or costs associated with thermoregulation) (Foa and Bertolucci 2001; Garcia-De la Pena *et al.* 2007). Variation in seasonal activity patterns in lizards are therefore with no surprise, generally associated with resource availability in combination with thermal regimes (Huey 1982; Davis and DeNardo 2009; Davis and DeNardo 2010), whereas other factors such as predation (McFarland 1976) and circadian rhythms (Winne and Keck 2004) may also have an effect on activity. *Cordylus cataphractus* is reported to remain within crevices (i.e. show reduced surface activity) for prolonged periods during the dry late summer and autumn as well as winter months, sometimes sitting with only their heads protruding or outside within 0.1 m from crevice edges (Visagie 2001). *Cordylus cataphractus* undergoes severe food limitation (stress) during the prolonged dry season (late summer to autumn), likely due to the combination of site specificity, a group-living life strategy and sit-and-wait foraging mode in a semi-arid habitat (Mouton *et al.* 2000a; Visagie 2001; Flemming and Mouton 2002; Effenberger and Mouton 2007; Hayward 2008). The lowered surface activity reported for *C. cataphractus* during the dry season (late summer to autumn) has been linked to the low food availability in combination with their group-living life strategy (Visagie 2001; Hayward 2008).

The contribution of seasonal trends in the thermal environment on seasonal surface movement patterns of *C. cataphractus* however remains unexplored.

Reptiles may thermoregulate behaviourally within retreat sites by modifying body postures to either increase or decrease surface contact (Cowles and Bogert 1944; Huey 1982), by selecting thermally favourable microsites, and/or through social huddling (during cold periods) when individuals press closely together to increase the total mass, therefore decreasing the surface to volume ratio and subsequent cooling rates (Lanham 2001; Shah *et al.* 2003). The fact that *C. cataphractus* individuals are often positioned on crevice edges or with only their heads protruding during the warm dry season (Visagie 2001; Hayward 2008) suggests that they are active and not in deep aestivation during unfavourable times. It however remains unknown whether *C. cataphractus* individuals actively regulate their body temperatures as opposed to conforming to temperatures in the crevice during the prolonged periods spent within the shade of crevices.

The primary objective of the current study was to provide a detailed description of the thermal habitat of a *C. cataphractus* population during summer, autumn, winter and spring and relate these findings to patterns of thermoregulation as well as the seasonal activity patterns reported in the literature for the species.

The specific questions addressed by the study were:

1. How does the thermal habitat quality of *C. cataphractus* vary at micro-spatial scale (i.e. around rocks) as a function of the time of day and time of year (i.e. season)?

2. Does variation in thermal habitat quality around rocks provide an incentive for intra group competition?

3. Does *C. cataphractus* exhibit lowered diel and annual activity periods due to thermal constraints?

4. Are the seasonal activity and movement patterns on rock surfaces as reported in the literature for *C. cataphractus* related to thermal factors?

3.3 Materials and Methods

3.3.1 Study area and animals

The study site is situated on a range of sandstone ridges adjacent to the Verlorenvlei Estuary near Elands Bay (32°19'38.61"S; 18°21'35.78"E) on the South African West Coast. The population of *C. cataphractus* sampled, consists of numerous social groups of between two and 25 individuals (Visagie 2001). The area is semi-arid (~200 mm per annum) being characterized by a prolonged dry season during the warm summer and autumn months, whereas winter and spring are cooler and less arid (rainy season) (Figure 3.1) (South African Weather Service; Mucina and Rutherford 2006). Aridity is reduced by dew and morning fog originating from the cold Benguela Atlantic Current (Mucina and Rutherford 2006; van Rensburg *et al.* 2009). Although fog occurs frequently during the warm dry months of March, April and May, it mostly dissipates by 9h00 (Olivier 2002). The vegetation type is Langebaan Dune Strandveld and hosts an array of perennial herbaceous flora that emerges during spring (Mucina and Rutherford 2006). These flower blooms sustain a high diversity of nectar and pollen feeding invertebrates (Struck 1994).
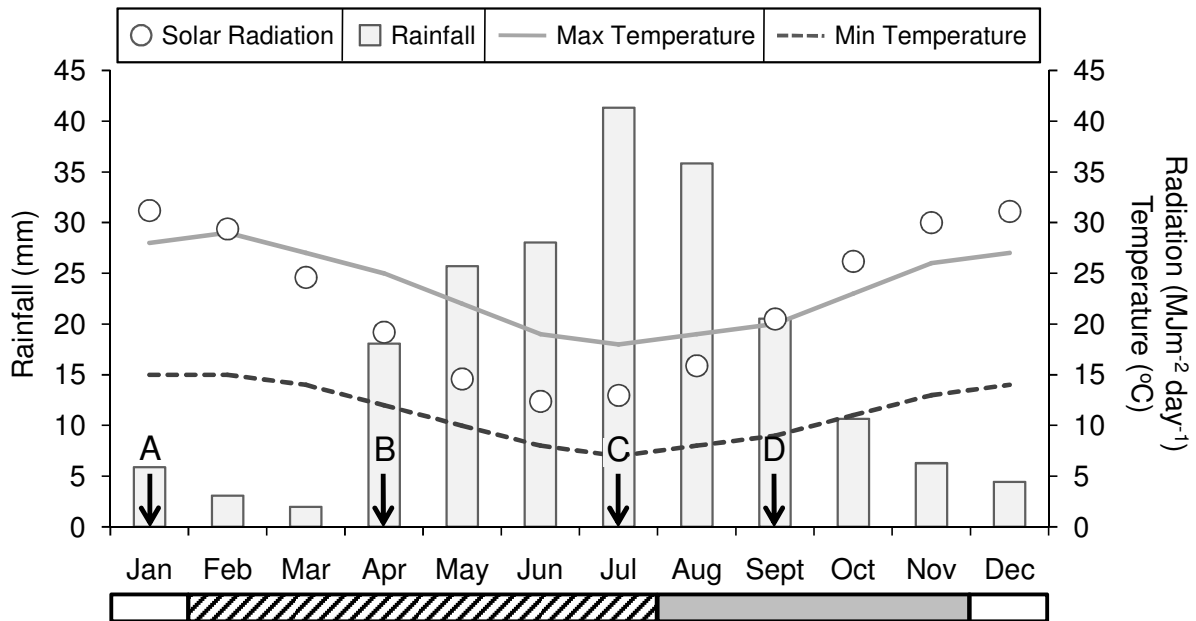
Figure 3.1. Monthly mean estimates of solar radiation, minimum ambient temperature and maximum ambient temperature (A van Niekerk, unpublished data) and mean precipitation for Elands Bay (rainfall: 1998-2008, SA Weather Services). Vertical arrows indicate the respective sampling periods (A: summer; B: autumn; C: winter; D: spring). The horizontal bar indicates the seasonal activity of *C. cataphractus* as described in the literature (Visagie 2001; Effenberger and Mouton 2007) (slanted-line: repressed activity; grey: normal surface activity; clear: activity unknown).

3.3.2 Operative environmental temperature (T_e) and thermal habitat quality (d_e)

3.3.2.1 T_e-models

Operative environmental temperatures (T_e) were measured in the field with hollow copper models that matched lizards in size, shape and reflective properties (Bakken 1992). The models used in this experiment were the same ones used in the field trials of Chapter 4 of this thesis (coastal population). For the construction and calibration of models see Chapter 4, sections 4.3.2.1 and 4.3.2.2. The autumn and winter models were painted according to skin reflectance measured at 300 nm – 750 nm (due to equipment limitation), whereas the spring and summer models were painted according to 250 nm – 2500 nm (see section

4.3.2.1). All models were calibrated using the appropriate regression equations described in section 4.3.2.2.

3.3.2.2 T_e-model placement

The T_e-models were positioned among the aspects of rocks (typically inhabited by *C. cataphractus*) which directly faced one of the four main wind directions (i.e. North, East, South and West). The rationale was to use aspects from different rocks which when combined, would express the thermal habitat of *C. cataphractus* around a single hypothetical rock. Each direction was represented by aspects from a minimum of three and a maximum of five different rocks. Models were positioned at varying distances from crevices, i.e. 0 m, 0.1 m, 0.3 m, 0.5 m, 0.7 m and 0.9 m respectively in accordance with natural movement patterns described for *C. cataphractus* (Effenberger and Mouton 2007). At least three additional models were placed deep within rock crevices to measure T_e-min. Crevices were thermally mapped in more detail during the summer field trial by placing 27 additional T_e-models beneath rocks. These models were positioned at variable distances from the crevice edge (50 mm to 0.6 m) beneath four rocks inhabited by *C. cataphractus*. The approximate rock thickness, crevice height, distance from rock edge and distance from crevice edge were noted for the position of each T_e-model.

Operative temperatures (T_e) were recorded at 15 minute intervals for 14 days during the autumn (April), winter (July) and spring (September) of 2008 and the summer (January) of 2009. All abnormally windy or non-representative days were excluded leaving 11 days in summer, nine in autumn, 10 in winter and four in spring. Four abnormally hot days were observed in summer and two in winter, which were analysed separately. The data for several models were lost due to either iButton failure or T_e-models that were damaged, moved, or carried off by wild and/or domestic animals. In this study data were eventually collected from 44 T_e-models in summer, 21 in autumn, 27 in winter and 28 in spring.

3.3.3 Field body temperatures (T_b)

Seven adult lizards were fitted with Thermochron iButtons (Dallas Semiconductor, USA), modified according to the Robert and Thompson (2003)-protocol. The protocol was further customized, specifically, by rearranging the electronic components and placing the battery alongside the electronic unit; logger thickness was further reduced to 3.8 mm (see Chapter 2, section 2.1.3). The loggers were waterproofed and attached to the dorsal body surface of the lizard using super glue gel (Henkel Pattex, DE).

Lizard body temperatures were recorded during the corresponding period of logging as operative temperatures (T_e) at 15 minute intervals for 14 days during the autumn (April), winter (July) and spring (September) of 2008 and the summer (January) of 2009. iButtons were left attached to lizards throughout the experimental trial where possible. The data from various lizards were however lost due to faulty iButtons, or lizards that could not be retrieved. Faulty iButtons were carefully removed and replaced, whereas unrecovered individuals were substituted during the following season. Ultimately data were obtained for six lizards in summer (M3:F3, male:female), seven in autumn (M2:F5) and three in both winter (M1:F2) and spring (M1:F2). All the recorded body temperatures were adjusted using the calibration function estimated in Chapter 2, section 2.3.2.2, thus adjusting T_b-measurements taken on the skin surface to the predicted cloacal T_b.

3.3.4 Lizard activity

A one-day scan sampling (Altmann 1974) was performed during autumn to provide an anecdotal estimate of the surface activity of *C. cataphractus* at the time. Effenberger and Mouton (2007) performed a focal scan on *C. cataphractus* during spring which included reports of thermoregulatory activity. Although Visagie (2001) studied the behaviour of *C. cataphractus* during autumn, winter and spring and reported that lizards predominantly remained on the edge of or within crevices during autumn, she did not report on thermoregulatory (basking) activity. The current results should however be interpreted with caution because of the small sample size.

A single group containing 20 lizards was monitored with a telescope (Magnum 345, Bushell, SA) from a distance of approximately 30 metres. The observations took place from 8h00 to 19h00 on a clear sunny day. Three 15 minute observations were performed during each hour of the day, during which the sun exposure, orientation relative to the sun, posture, distance from crevice and general behaviour was noted for every lizard visible. Most of the lizards remained deep within crevices and could therefore not be monitored. Some of the individuals that were visible performed thermoregulatory activity at certain stages (adjusting posture and orientating themselves relative to the sun), yet mostly on the edges of crevices or just within or outside them.

3.3.5 Data analysis and statistics

3.3.5.1 Calculation of thermoregulation indices

(1) Thermal habitat quality (d_e) (Hertz et al. 1993)

The degree to which T_e deviates from T_p describes thermal suitability from the organism's perspective and hence thermal quality. The thermal quality index (d_e) also reflects on the costs of thermoregulation, high absolute value of d_e representing a potential high cost in a low thermal quality environment (hot or cold). Thermal habitat quality (d_e) is calculated from the absolute deviation of T_e from T_p ($d_e = [T_e -$ upper limit of $T_p]$, if $T_e > T_p$: $d_e = $ [lower limit of $T_p - T_e]$, if $T_e = T_p$, $d_e = 0$).

(2) Accuracy of thermoregulation (d_b) (Hertz et al. 1993)

Accuracy of thermoregulation expresses the degree to which T_bs attained in the field match the target preferred temperature (T_p) range. Thermoregulatory accuracy is calculated from the absolute deviation of T_b from T_p ($d_b = [T_b -$ upper limit of $T_p]$, if $T_b > T_p$: $d_b = $ [lower limit of $T_p - T_b]$, if $T_b = T_p$, $d_b = 0$). A high d_b-value therefore expresses low accuracy whereas $d_b = 0$ represents a perfect match (Hertz *et al.* 1993).

(3) Effectiveness of thermoregulation (d_e – d_b) (Blouin-Demers and Weatherhead 2001)

When thermal quality is high (i.e. low d_e), lizards may accurately maintain T_b within T_p with little or no associated thermoregulatory costs (i.e. passive thermoconformation). It is therefore essential to consider accuracy (d_b) as a function of thermal quality (d_e) in order to establish the amount of- or effectiveness of active thermoregulation performed.

Hertz *et al*. (1993) described the index for effectiveness of thermoregulation (E), calculated as: $E = 1 - (d_b/d_e)$. The E-index has however been criticized due to its ratio nature as well as the fact that it is undefined when $d_e = 0$ (Christian and Weavers 1996; Blouin-Demers and Weatherhead 2001; Blouin-Demers and Weatherhead 2002). As an alternative, Blouin-Demers & Weatherhead (2001) described an index for the effectiveness of thermoregulation (d_e – d_b), simply calculated as the difference between d_e and d_b. In principle, both the d_e – d_b and E describe the same dimension of thermal ecology, i.e. the degree of departure from thermoconformity (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Weatherhead 2002). A d_e – d_b of zero indicates thermoconformation, and the extent of increase reflects the amount of active thermoregulation performed.

(4) Thermal exploitation (E_x)

The E_x metric describes the extent to which favourable thermal opportunities available to an animal are exploited by it (E_x = (time in which $T_b = T_p$ / time in which $T_e = T_p$) x 100%) (Christian and Weavers 1996).

The preferred temperature range (T_p) of the population examined in the current study was estimated in a laboratory thermal gradient during the autumn and spring of 2008 (Chapter 2). Although T_p was slightly lower in autumn, the difference was not significant. The current study employed the respective T_p ranges estimated for autumn and spring in the indices of the appropriate season, whereas the mean preferred temperature range (T_p) for *C. cataphractus* (Chapter 2) was employed for the summer and winter computations.

3.3.5.2 Statistical analysis

Temporal autocorrelation of data was assessed with Time Series Analysis (STATISTICA 8, Statsoft Inc., USA). Typically, temperatures taken 30 minutes apart were independent of each other for both T_e and T_b. Normality of data was assessed with the Shapiro-Wilk's W-test or Kolmogorov-Smirnov when datasets exceeded 2000 values. Transformations did not improve normality and was subsequently not used.

Generalized linear mixed model analyses (PROC GLIMMIX, SAS 9.1, SAS Institute Inc., USA) with experimental day as repeated measure was used (since both T_e and T_b data were repeated measures across days, unbalanced due to missing values and residuals were in many cases not normally distributed). The compound symmetry (CS) covariance structure was used (Littell *et al.* 1996). Analyses were performed on hourly means calculated from measurements taken at 15 minute intervals (7h00 – 19h00) leaving 12 hourly mean values per day per season for each experimental unit (i.e. model or lizard). Although some of the lizards were used during more than one season, these were in the minority and lizards were therefore assumed as independent among seasons.

A non-parametric bootstrap ANOVA (x1000 iterations) (Efron 1993) (performed on hourly means calculated per season for each lizard unit) was applied for the thermal exploitation index (E_x) since the index was calculated across days and therefore lacks "experimental day" as repeated measure.

Data were analyzed using SAS Enterprize Guide 3, SAS 9.1 (SAS Institute Inc., USA) and STATISTICA 8 (Statsoft Inc., USA). Means are reported ± one standard deviation (SD). Probability values (*P*) of less than 0.05 were accepted as significant, whereas $P < 0.01$ indicates highly significant effects.

3.4 Results

3.4.1 Operative environmental temperature (T_e) and thermal habitat quality (d_e)

3.4.1.1 Among-seasons comparison

Both the hourly mean operative environmental temperatures (T_e) and the resultant thermal habitat quality (d_e) were significantly affected by the time of day (i.e. hour) (T_e: $F_{11,1298}$ = 1151.2, P < 0.01; d_e: $F_{11,1298}$ = 379.56, P < 0.01), field-trial day (T_e: $F_{10,943}$ = 74.7, P < 0.01; d_e: $F_{10,943}$ = 22.49, P < 0.01) and season (T_e: $F_{3,115}$ = 66.87, P < 0.01; d_e: $F_{3,115}$ = 119.43, P < 0.01). Moreover, the least square means post hoc analyses indicated that both T_e and d_e (deviation of T_e from T_p) (7h00 – 19h00) varied significantly (pair-wise) between the respective seasons (P < 0.01, Tukey-Kramer), with the exception of summer and autumn in which T_e and d_e corresponded relatively to each other (T_e: P = 0.06; d_e: P = 0.63, Tukey-Kramer) (Figure 3.2; Appendix Table A1). Operative environmental temperatures were highest and most favourable (lowest d_e) during autumn, followed by summer, spring and winter (Figure 3.2). The hourly pattern of mean d_e correspond relatively among summer and autumn throughout the day, being lower than that of spring and markedly lower than the d_e of winter (Figure 3.2; Appendix Table A1). The mean d_e reached a minimum (indicating high thermal habitat quality) during summer and autumn from 17h00 to 19h00 (d_e < 2°C) (Figure 3.2).
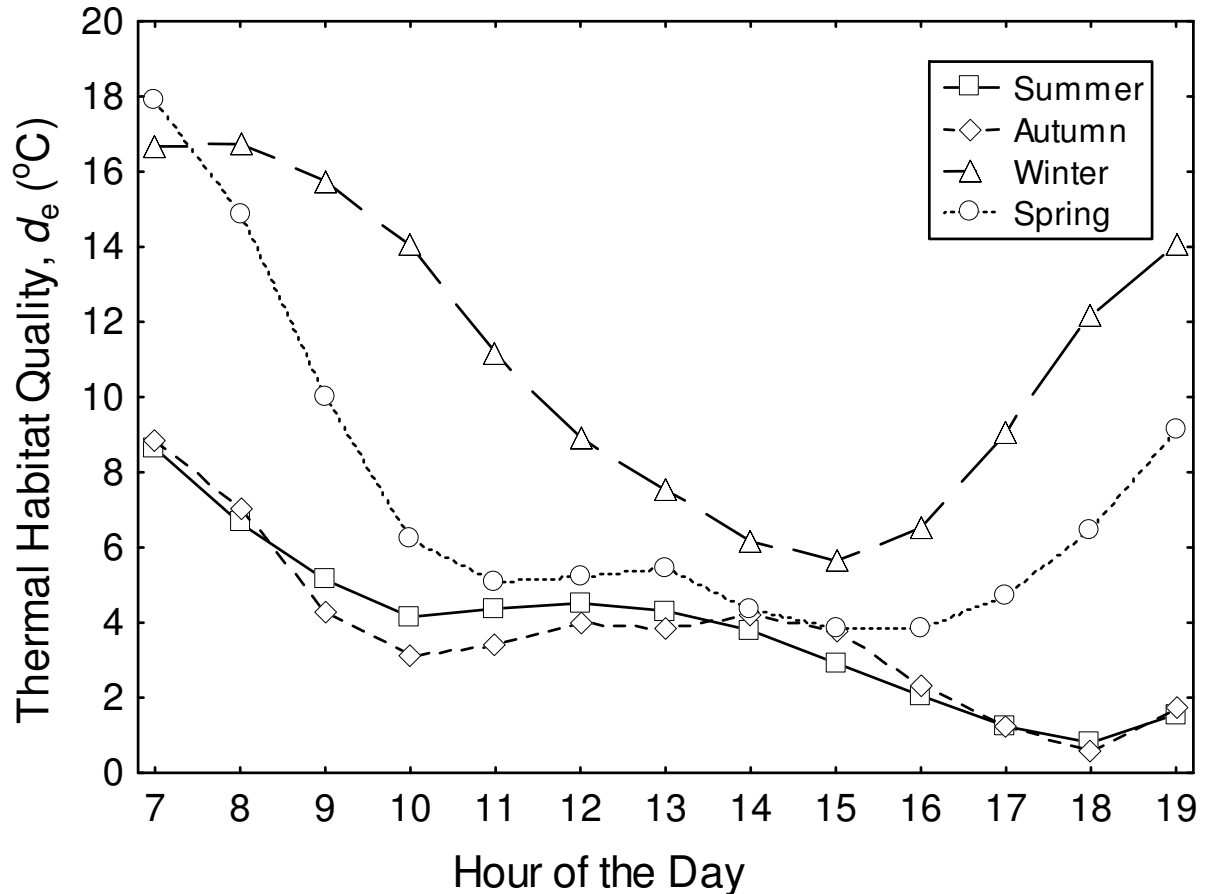
Figure 3.2. Seasonal comparison of hourly variation in the mean thermal habitat quality (d_e) of a coastal population of *C. cataphractus*. Thermal habitat quality is expressed as the degree of deviation of operative environmental temperatures (T_e) from the preferred temperature range (T_p). A d_e of zero indicates perfect thermal habitat quality (i.e. $T_e = T_p$) suggesting the potential of passive thermoconformation (Hertz *et al.* 1993). The hourly means ± 1SD of d_e is given in Appendix Table A2.

3.4.1.2 Summer

Typical summer days

Mean operative environmental temperatures (T_e) were favourable in summer, equalling the preferred temperature range (T_p) from 11h00 to 18h00 (overall mean T_e = 28.3 $^{\circ}$C ± 7.0 $^{\circ}$C) (Figure 3.3). Mean crevice T_es were significantly lower and less favourable than mean T_es in the open (P < 0.01, Tukey-Kramer), and typically equalled T_p from 14h00 to 18h00 (Figure

3.3). The frequency distribution of T_es outside of crevices indicated a moderate overlap with T_p, in particular, 19.8 % of T_es equalled T_p, 52.1 % were higher and 28.1 % lower (7h00 – 19h00) (Figure 3.4). Of the T_es measured within crevices, 30.2 % were within T_p, 66.8 % below, and only 3.0 % higher than T_p (7h00 – 19h00) (Figure 3.5). Thermal habitat quality was relatively favourable during typical summer days (overall mean d_e = 3.5 °C ± 3.7 °C) (Figure 3.2).
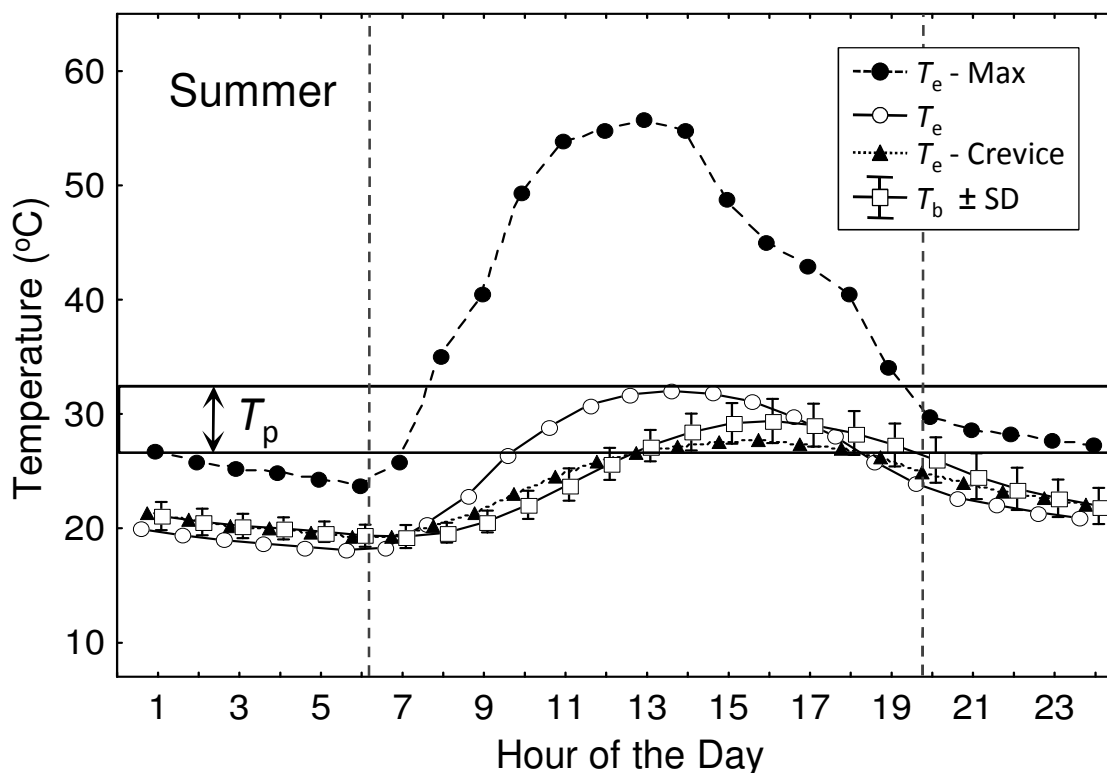
Figure 3.3. Hourly means of operative environmental temperatures (T_e), field body temperatures (T_b ± 1SD) and crevice T_es, and the absolute maximum observed T_es (T_e-max) recorded for a coastal *C. cataphractus* population during 11 typical summer days. The horizontal rectangle depicts the preferred temperature range (T_p). Vertical dotted lines indicate sunrise and sunset (South African Astronomical Observatory). Standard deviations are indicated only for T_b for clarity purposes (of the figure). The hourly means ± 1SD of T_e, T_e-crevice and T_b are given in Appendix Tables A3, A4 and A5.
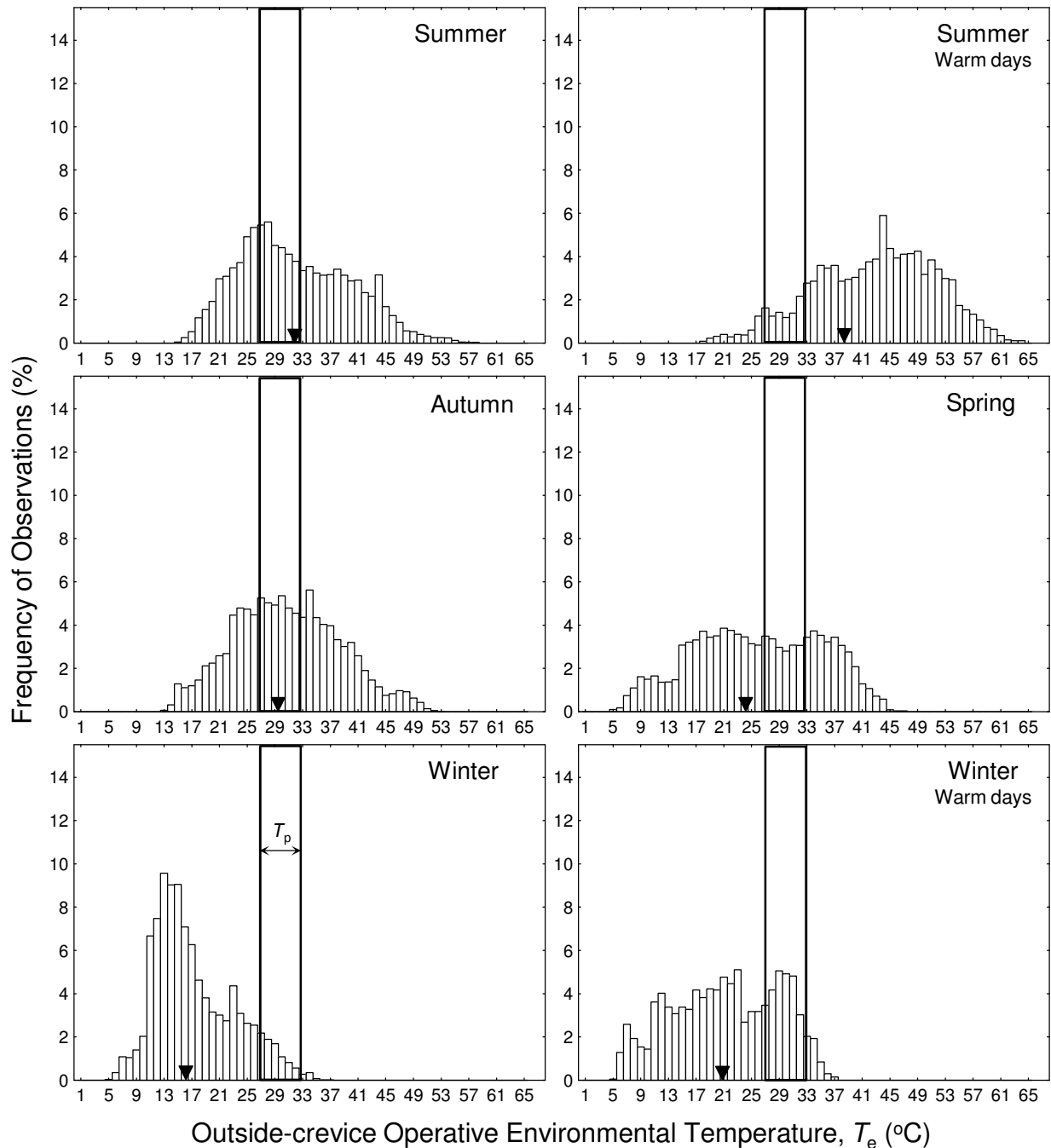
Figure 3.4. The frequency distributions of operative environmental temperatures (T_e) recorded outside of crevices during summer, four abnormally warm summer days, autumn, spring, winter and two abnormally warm winter days (7h00 – 19h00) for a coastal population of *C. cataphractus*. Arrow heads indicate overall mean T_e, whereas the vertical rectangles depict the preferred temperature range (T_p) of *C. cataphractus* (N = 18 models in summer, 14 autumn; 21 winter and 21 spring).
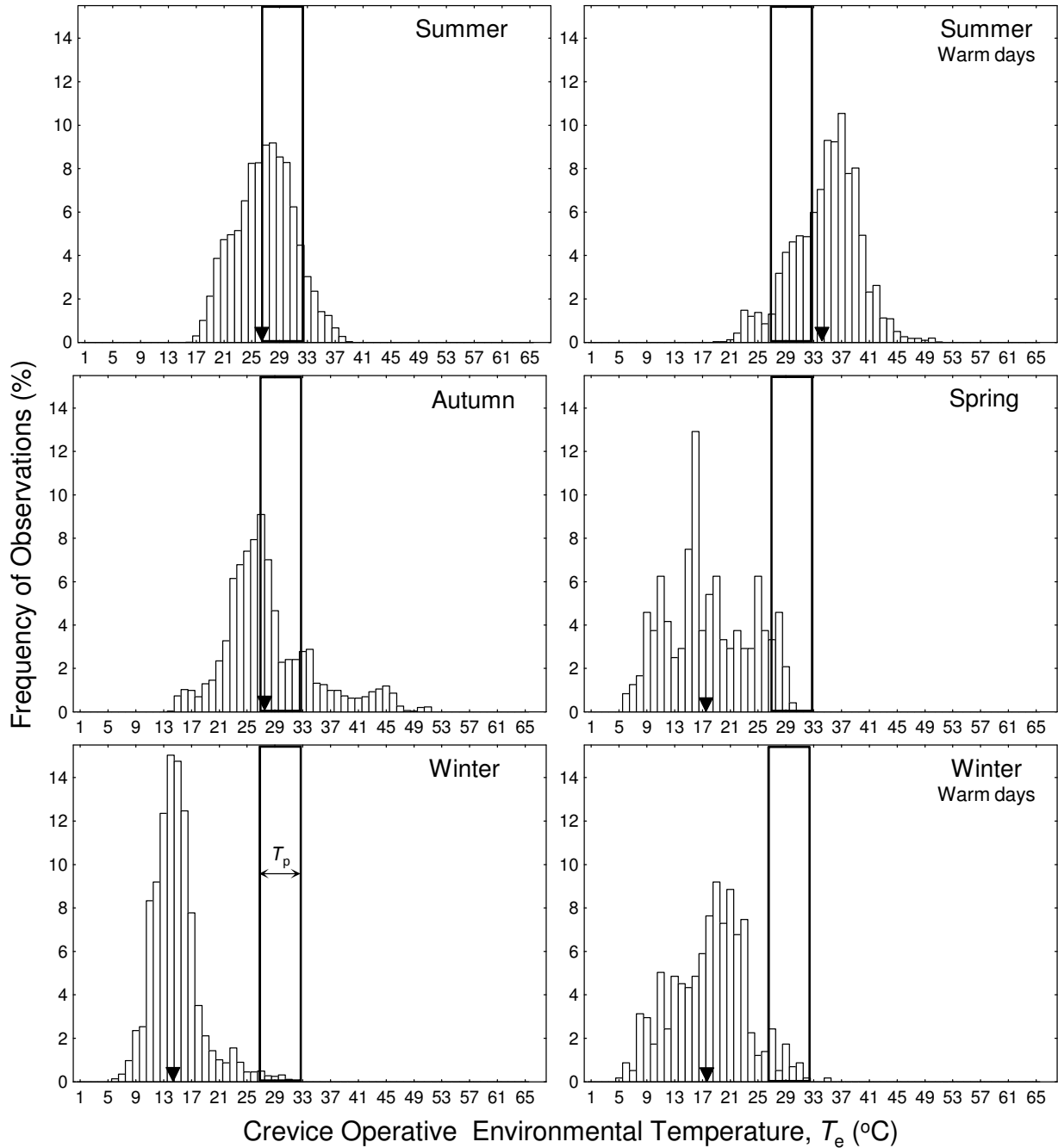
Figure 3.5. The frequency distributions of operative environmental temperatures (T_e) recorded on the edges of and within crevices during summer, four abnormally warm summer days, autumn, spring, winter and two abnormally warm winter days (7h00 − 19h00) for a coastal population of *C. cataphractus*. Arrow heads indicate overall mean T_e, whereas the vertical rectangles depict the preferred temperature range (T_p) of *C. cataphractus* (N = 26 models in summer, seven in autumn, six in winter and seven in spring).
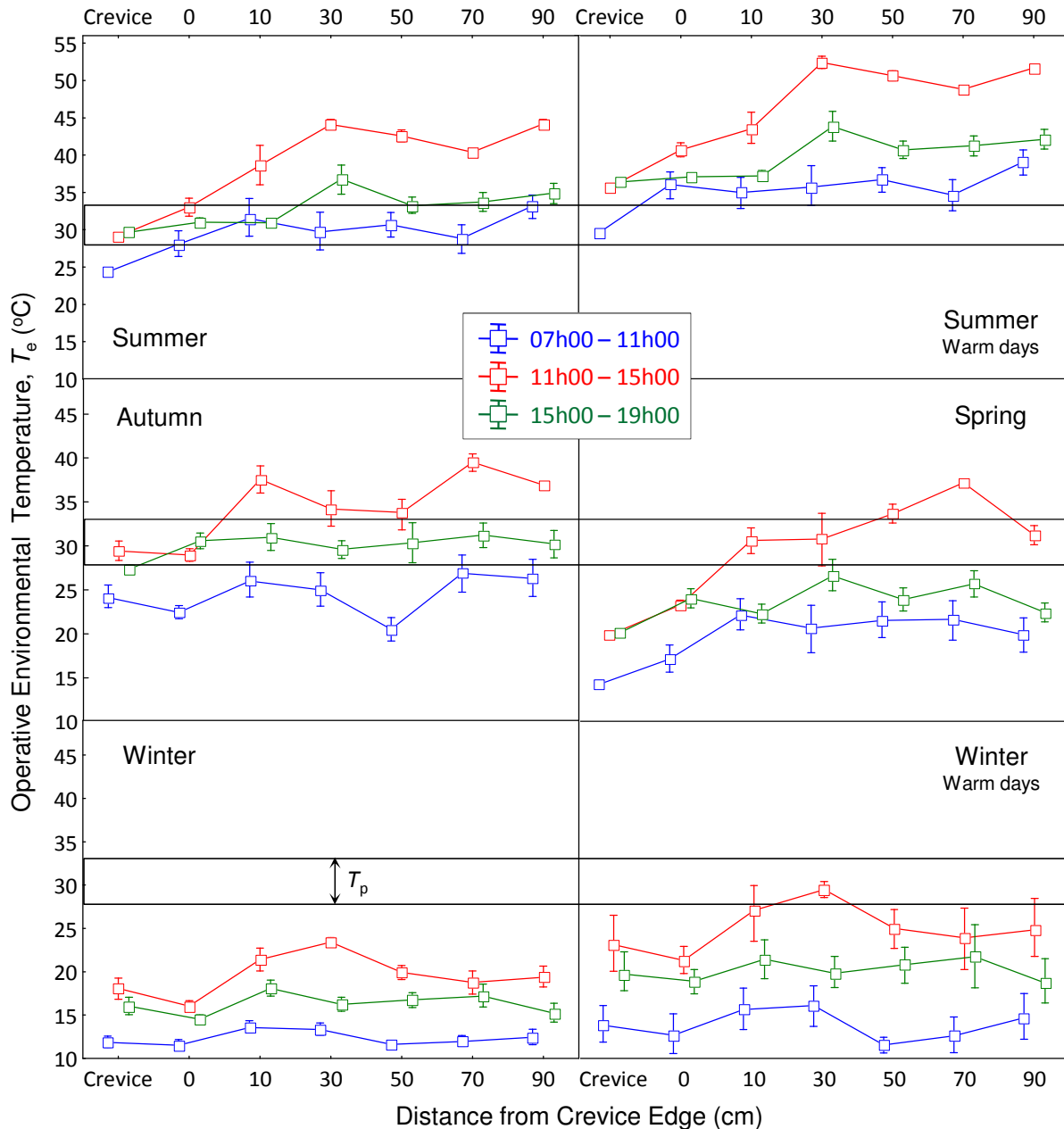
Figure 3.6. Mean operative environmental temperatures (T_e) as a function of distance from crevice edge, recorded seasonally in a coastal population of *C. cataphractus* during the respective morning (7h00 – 11h00), midday (11h00 – 15h00) and afternoon (15h00 – 19h00) time intervals. Data points represent mean T_e values calculated from hourly means representing the respective diel segments. Vertical bars denote 95 % bootstrap confidence intervals (1000 iterations). Horizontal rectangles indicate the preferred temperature range (T_p) of *C. cataphractus*.

Mean operative environmental temperatures (T_e) varied significantly as a function of distance from crevice in summer ($F_{6,36}$ = 15.79, P < 0.01), as well the time of day (i.e. hour) ($F_{11,396}$ = 1059.17, P < 0.01; Figure 3.6). Mean T_es were lowest within crevices during the morning period (on average being lower than T_p), but were relatively invariable among distance classes outside of crevices, and only the models placed 0.9 m from crevices (in the open) typically exceeded T_p temperatures (Figure 3.6). During midday, mean T_e increased as a function of distance from crevice, exceeding T_p at all but the "crevice" distance classes (i.e. 0 m, 0.1 m, 0.3 m, 0.5 m, 0.7 m, 0.9 m), whereas, during the afternoon, T_p was only available within crevices and up to 0.1 m in the open (see Figure 3.6).

Mean operative environmental temperatures varied significantly among rock aspects facing the four wind directions (i.e. around rocks) ($F_{3,17}$ = 3.97, P = 0.03; Figure 3.7), in particular being highest and least thermally favourable at the eastern aspects followed by west, south and north (see Figure 3.7). The only significant pair-wise difference in mean T_e was between the eastern and northern rock aspects (P = 0.05, Tukey-Kramer). Although the mean thermal habitat quality (d_e) varied accordingly, being lowest (higher d_e) on the eastern aspects (Table 3.1), mean d_e of eastern aspects differed significantly only from the southern aspects (P < 0.01, Tukey-Kramer).

The thermal habitat within crevices was explored in more detail during summer (27 T_e-models beneath rocks in crevices) than autumn, winter and spring, and mean operative environmental temperatures varied significantly as a function of distance from crevice edge ($F_{13,9.51}$ = 22.96, P < 0.01), relative rock thickness ($F_{9,14.3}$ = 228.44, P < 0.01) and crevice height ($F_{8,15.65}$ = 35.96, P < 0.01) (PROC GLIMMIX using Satterthwaite denominator degrees of freedom).
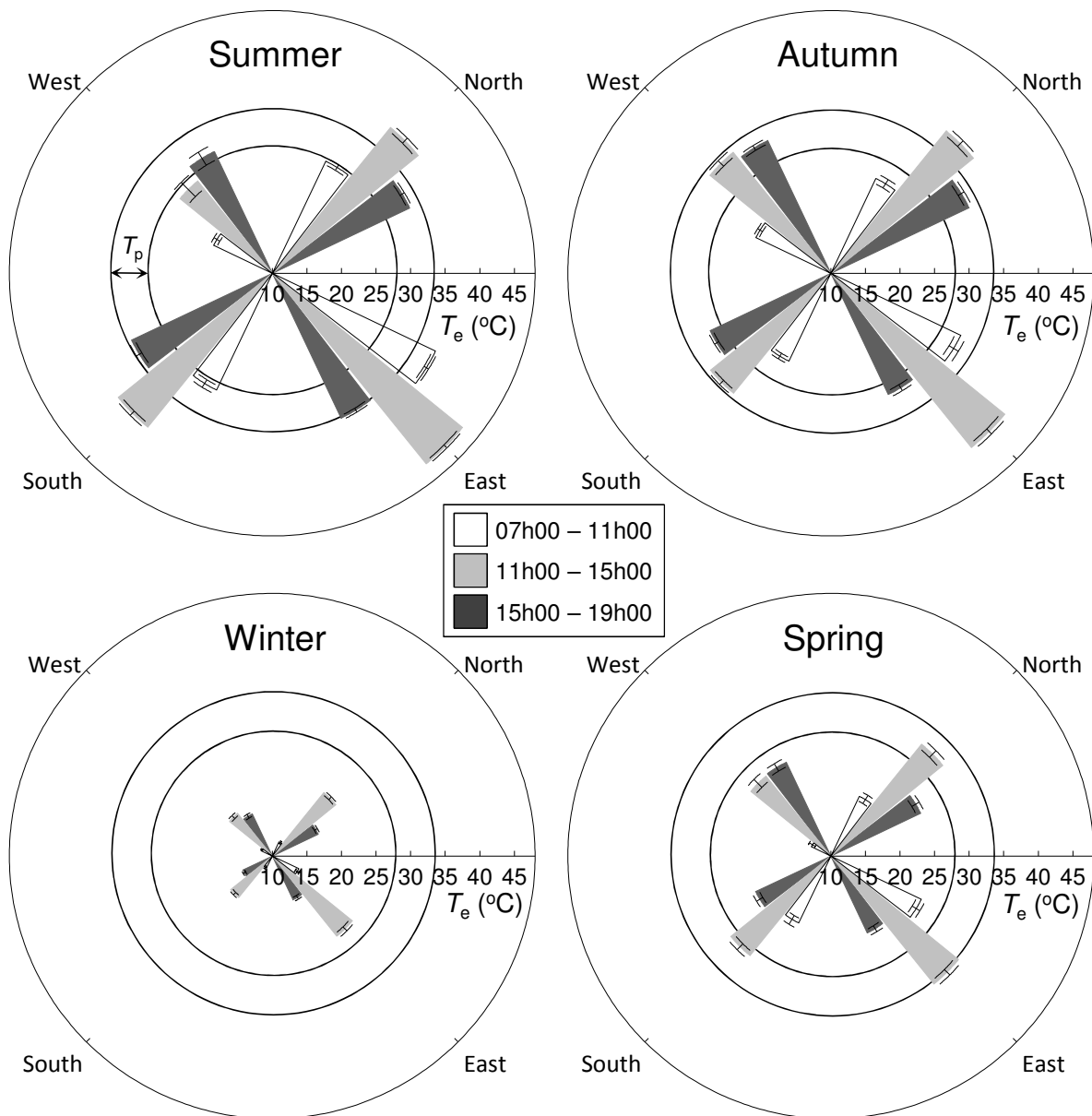
Figure 3.7. Mean operative environmental temperatures (T_e) observed among rock aspects representing the four major wind directions, during summer, autumn, winter and spring (7h00 – 19h00) (N = 8 rocks, 14 aspects) in a coastal population of *C. cataphractus*. The internal rings depict the preferred temperature range (T_p) of *C. cataphractus*. Vertical bars denote 95 % bootstrap confidence intervals (1000 iterations) calculated from T_es measured at 15 minute intervals.

Table 3.1. Variation in the overall mean thermal habitat quality (d_e) of a coastal population of *C. cataphractus* among different rock aspects (facing the four major wind directions) (i.e. NESW) across seasons (7h00 – 19h00). A d_e value of zero indicates a perfect match of mean T_e and the preferred temperature range (T_p) (and therefore good thermal habitat quality) (i.e. $T_e = T_p$) (Hertz *et al.* 1993).

Season	d_e (°C)			
	North	East	South	West
Summer	4.1 ± 3.6	5.9 ± 5.6	2.1 ± 2.9	4.2 ± 3.2
Warm summer days	9.5 ± 7.4	11.8 ± 7.9	8.5 ± 5.5	9.2 ± 7.3
Autumn	3.7 ± 3.9	5.2 ± 5.1	2.3 ± 3.1	3.6 ± 3.7
Winter	9.8 ± 5.6	8.6 ± 5.7	12.0 ± 4.0	11.3 ± 4.4
Warm winter days	6.5 ± 6.7	5.8 ± 6.0	8.9 ± 5.6	8.5 ± 6.3
Spring	6.2 ± 5.4	4.8 ± 4.2	5.4 ± 5.4	8.6 ± 6.5

Exceptionally warm summer days

Four exceptionally hot days were observed during the summer field trial during which (unlike the typical summer days) the mean T_e exceeded T_p for most of the day (10h00 – 20h00) (overall mean T_e = 37.5 °C ± 7.8 °C) and the highest recorded T_e was 63.6 °C. In fact, the T_e-data suggest that it was virtually impossible for lizards to maintain T_bs within T_p during both the midday and afternoon periods (Figures 3.6 and 3.8). Mean T_e outside of crevices exceeded T_p from 9h00 to 19h00 and even mean crevice T_es exceeded T_p for the majority of the day (11h00 – 21h00) (Figure 3.8). The frequency distribution of T_es indicated a definite mismatch between T_e and T_p, in particular, 8.8 % of the outside-crevice T_es were within the preferred range (T_p), 85.7 % higher and only 5.6 % lower than T_p (7h00 – 19h00) (Figure 3.4). Of the T_es measured within crevices, 24.7 % were within T_p, 68.5 % higher and 6.9 % lower than T_p (7h00 – 19h00) (Figure 3.5). Following high T_es, thermal habitat quality (d_e) was poor during these warm days (overall mean d_e = 6.1 °C ± 6.5 °C), being significantly higher within crevices than in the open (d_e: crevice = 3.1 °C ± 3.0 °C, open = 10.5 °C ± 7.5 °C) ($F_{1, 7419}$ = 575.40, $P < 0.001$).
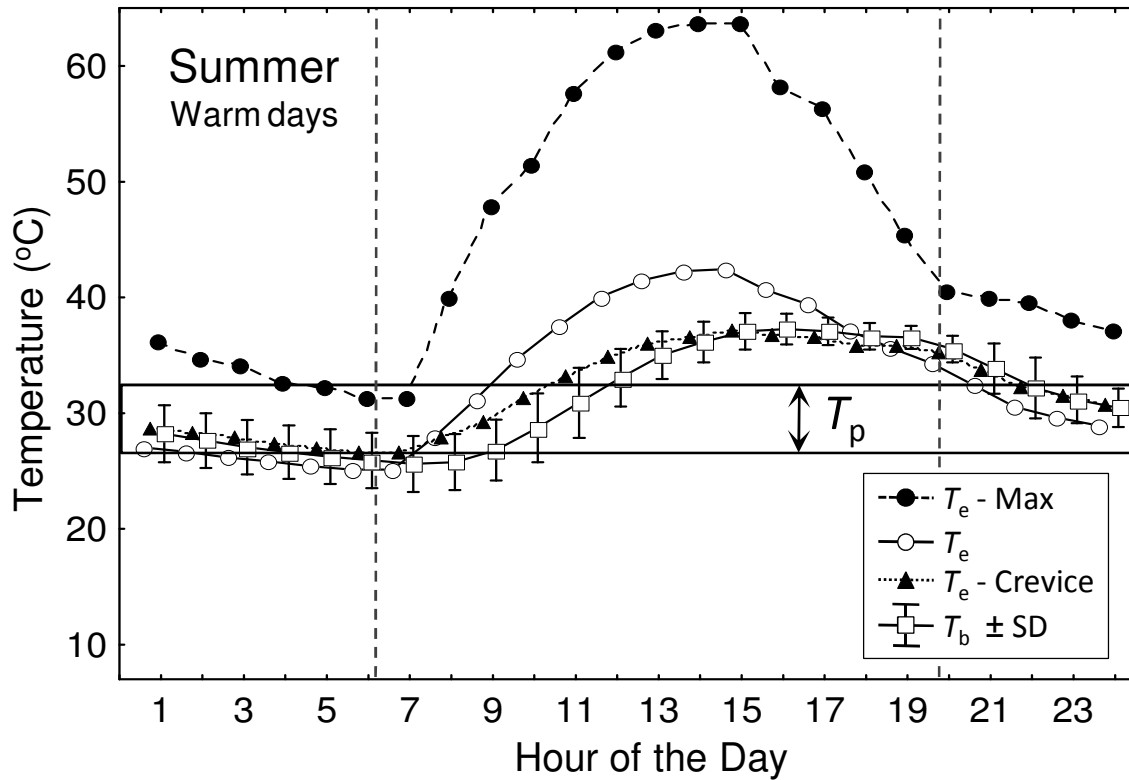
Figure 3.8. Hourly means of operative environmental temperatures (T_e), field body temperatures ($T_b \pm 1SD$) and crevice T_es, and the absolute maximum observed T_es (T_e-max) recorded for a coastal *C. cataphractus* population during three abnormally hot summer days. The horizontal rectangle depicts the preferred temperature range (T_p) (an overlap with T_e indicating good thermal quality, $d_e = 0$). Vertical dotted lines indicate sunrise and sunset (South African Astronomical Observatory). Standard deviations are indicated only for T_b for clarity purposes (of the figure). The hourly means $\pm 1SD$ of T_e, T_e-crevice and T_b are given in Appendix Tables A3, A4 and A5.
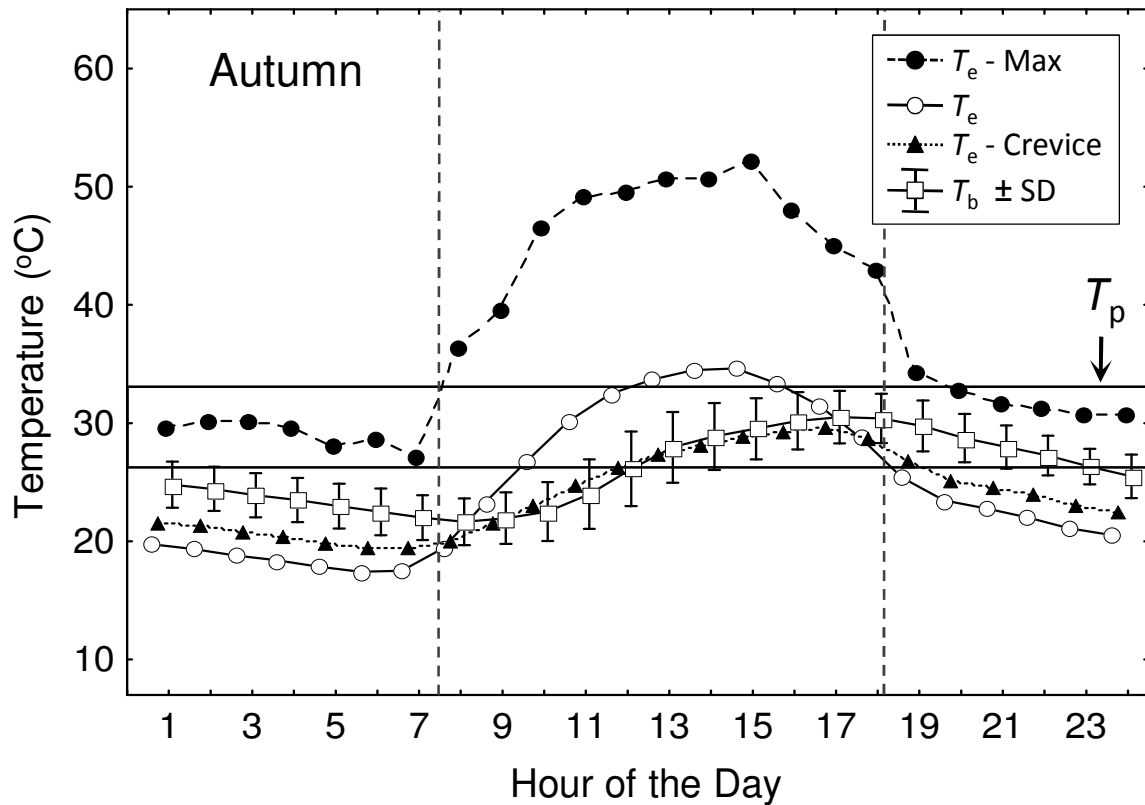
Figure 3.9. Hourly means of operative environmental temperatures (T_e), field body temperatures ($T_b \pm 1SD$) and crevice T_es, and the absolute maximum observed T_es (T_e-max) recorded during autumn in a coastal population of *C. cataphractus*. The horizontal rectangle depicts the preferred temperature range (T_p) (an overlap with T_e indicating good thermal quality, $d_e = 0$). Vertical dotted lines indicate sunrise and sunset (South African Astronomical Observatory). Standard deviations are indicated only for T_b for clarity purposes (of the figure). The hourly means $\pm 1SD$ of T_e, T_e-crevice and T_b are given in Appendix Tables A3, A4 and A5.

3.4.1.3 Autumn

Mean operative environmental temperatures (T_e) were favourable in autumn typically equalling T_p for five hours per day (10h00 – 12h00; 17h00 – 18h00) (overall mean T_e = 29.5 ^oC ± 7.5 ^oC) (Figure 3.9). Mean crevice T_es were significantly lower and more favourable than those in the open (P < 0.01, Tukey-Kramer), on average equalling T_p from 10h00 – 19h00 (Figure 3.9). The frequency distribution of T_es outside of crevices indicated a good match with T_p with numerous T_es within (28.3 %), above (42.2 %) and below T_p (29.6 %) (7h00 – 19h00) (Figure 3.4). Of the T_es measured within and on the edges of crevices, 37.2 % were within T_p, 53.6 % below, and 9.2 % higher than T_p (7h00 – 19h00) (Figure 3.5). Even though T_es were favourable in autumn, the index for thermal habitat quality (d_e) indicates only moderate suitability when collectively considering T_e in crevices and in the open (overall mean d_e = 3.3 ^oC ± 3.8 ^oC) (Figure 3.2). When viewed as a function of the time of day, d_e remained ~4 ^oC for the majority of activity time and reached a peak low at 18h00 (d_e < 1 ^oC) (Figure 3.2).

Mean T_e varied significantly as a function of distance from crevice edge in autumn ($F_{6,12}$ = 3.32, P = 0.04), and this "distance effect" was also significantly influenced by the time of day ($F_{11,132}$ = 337.85, P < 0.01; Figure 3.6; Appendix Table A9). In particular, during the morning interval, mean T_e was below T_p at all distance classes except 0.7 m, whereas, during midday, T_es within crevices and on crevice edges were typically within T_p while those outside of crevices generally exceeded T_p (see Figure 3.6). Conversely, during the afternoon, mean T_e equalled T_p in all distance classes (Figure 3.6).

Mean T_e varied significantly among rock aspects representing the four major wind directions ($F_{3,11}$ = 5.18, P = 0.02; Figure 3.7), in particular being significantly higher at the east-facing rock aspects than west (P = 0.02) and south (P = 0.03, Tukey-Kramer) respectively (Figure 3.7). As a result, the eastern aspects had the poorest thermal quality (d_e), yet only significantly so in relation to south (P = 0.01, Tukey-Kramer) (Table 3.1). The geographical variation in both T_e and d_e was also a function of the hour of the day ($F_{11,121}$ = 63.51, P < 0.01; Figure 3.7; Appendix Table A10).

3.4.1.4 Winter

Typical winter days

Mean operative environmental temperatures (T_e) were low in winter (overall mean T_e = 16.3 ^{o}C ± 5.4 ^{o}C) (Figure 3.10). The frequency distribution indicated an almost total mismatch between T_e and T_p both outside of and within crevices (Figures 3.4 and 3.5). In particular, 7.3 % of the T_es in the open equalled the preferred range (T_p), whereas 92.2 % were lower than- and only 0.4 % higher than T_p (7h00 − 19h00) (Figure 3.4). Of the T_es measured within crevices, 1.1 % was within T_p, 98.9 % below, and none higher (7h00 − 19h00) (Figure 3.5). Mean thermal habitat quality (d_e) was poor in winter (overall mean d_e = 10.6 ^{o}C ± 5.1 ^{o}C), being poorest at 7h00 and then increasing and peaking at 15h00 (Figure 3.2).

Distance from crevice edge had no significant effect on mean T_e during winter ($F_{6,18}$ = 1.87, P = 0.14; Appendix Table A9). Even when viewed as a function of the time of day, mean T_e was relatively invariable among distance classes during the morning and afternoon periods (Figure 3.6). The T_es of models that were 0.3 m away from crevices were most favourable during midday, yet still on average markedly below the target temperature range (T_p) (Figure 3.6).

Mean operative environmental temperatures varied significantly among rock aspects ($F_{3,18}$ = 10.22, P < 0.01) being most favourable at the east facing aspects, which were significantly higher and thermally more favourable than those at the southern (T_e and d_e: P < 0.01) and western aspects (T_e: P < 0.01; d_e: P = 0.01, Tukey-Kramer) (Figure 3.7; Table 3.1 and Appendix Table A10). In addition, mean T_e was significantly higher and more favourable at the northern than southern aspects (T_e: P = 0.02; d_e: P = 0.01, Tukey-Kramer; Figure 3.7).

Figure 3.10. Hourly means of operative environmental temperatures (T_e), field body temperatures ($T_b \pm 1SD$) and crevice T_es, and the absolute maximum observed T_es (T_e-max) recorded in a coastal population of *C. cataphractus* during nine typical winter days. The horizontal rectangle depicts the preferred temperature range (T_p) (an overlap with T_e indicating good thermal quality, $d_e = 0$). Vertical dotted lines indicate sunrise and sunset (South African Astronomical Observatory). Standard deviations are indicated only for T_b for clarity purposes (of the figure). The hourly means $\pm 1SD$ of T_e, T_e-crevice and T_b are given in Appendix Tables A3, A4 and A5.

Figure 3.11. Hourly means of operative environmental temperatures (T_e), field body temperatures ($T_b \pm 1SD$) and crevice T_es, and the absolute maximum observed T_es (T_e-max) recorded in a coastal population of *C. cataphractus* during two abnormally warm winter days. The horizontal rectangle depicts the preferred temperature range (T_p) (an overlap with T_e indicating good thermal quality, $d_e = 0$). Vertical dotted lines indicate sunrise and sunset (South African Astronomical Observatory). Standard deviations are indicated only for T_b for clarity purposes (of the figure). The hourly means $\pm 1SD$ of T_e, T_e-crevice and T_b are given in Appendix Tables A3, A4 and A5.

Warm winter days

Two warmer and thermally more favourable days were observed during the winter trial (overall mean T_e = 20.0 ^{o}C ± 7.3 ^{o}C) (Figures 3.4 and 3.11). Mean operative environmental temperatures typically equalled T_p from 13h00 to 16h00 (Figure 3.11). Although mean crevice T_e reached values exceeding 20 ^{o}C, it remained lower than T_p and lizards evidently would have had to emerge in order to attain T_b within T_p (Figures 3.6 and 3.11). The frequency distribution of the T_es observed in the open indicated only 2.0 % that exceeded T_p, whereas 20.7 % were within and 77.3 % below T_p (7h00 – 19h00) (Figure 3.4).

3.4.1.5 Spring

In spring, mean T_es typically equalled T_p from 12h00 to 16h00 (overall mean T_e = 24.3 ^{o}C ± 9.0 ^{o}C) (Figure 3.12). In contrast, mean crevice T_es remained lower than T_p throughout the day (Figure 3.12). The frequency distribution of T_e indicated a moderate overlap of T_es recorded outside of crevices with T_p, with 30.3 % of T_es above, 53.9 % below and 15.8 % within T_p (7h00 – 19h00) (Figure 3.4). In contrast, the frequency distribution of crevice T_es indicated an almost complete mismatch with T_p (Figure 3.5). In particular, 91.1 % were below, only 2.5 % above and 6.4 % within T_p (7h00 – 19h00) (Figure 3.5). The T_es recoded outside of crevices were significantly higher and more favourable than crevice T_es (P < 0.01, Tukey-Kramer). Thermal habitat quality was generally low in spring (overall mean d_e = 6.6 ^{o}C ± 5.6 ^{o}C). When viewed as a function of the time of day, mean d_e increased rapidly from 7h00 to 11h00 after which it stabilized slightly from 11h00 to 17h00 followed by a rapid decrease (Figure 3.2).
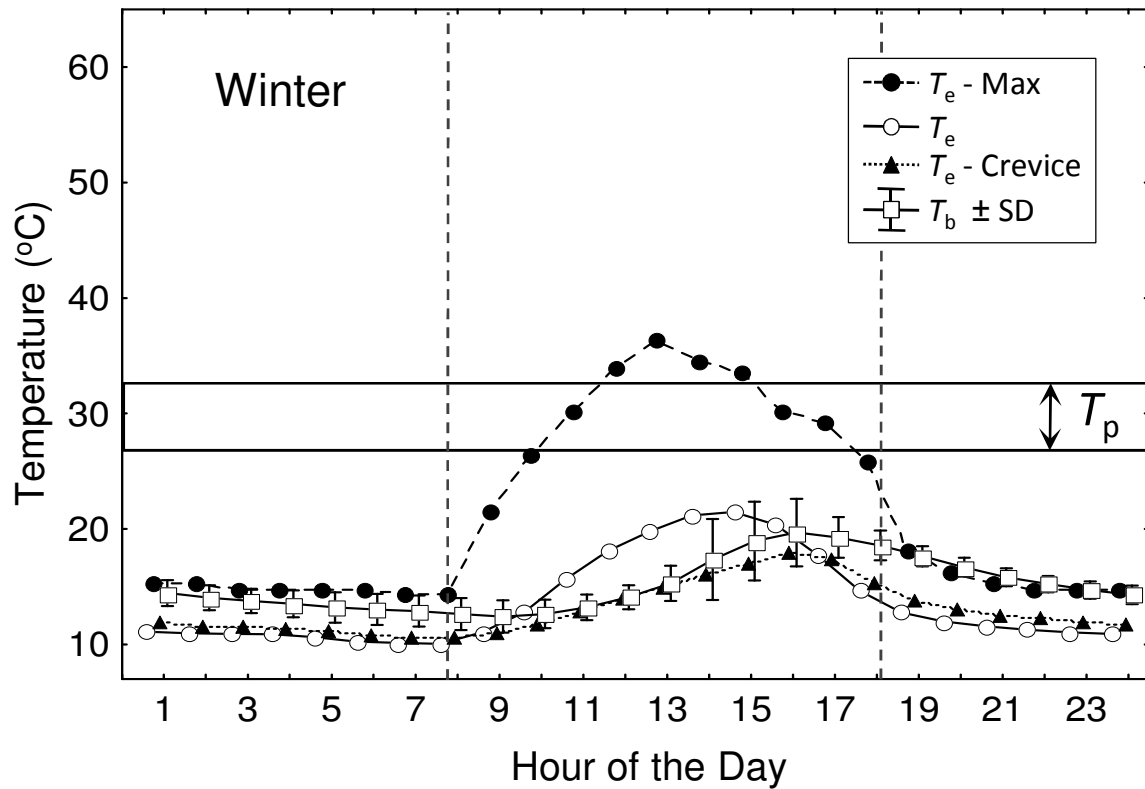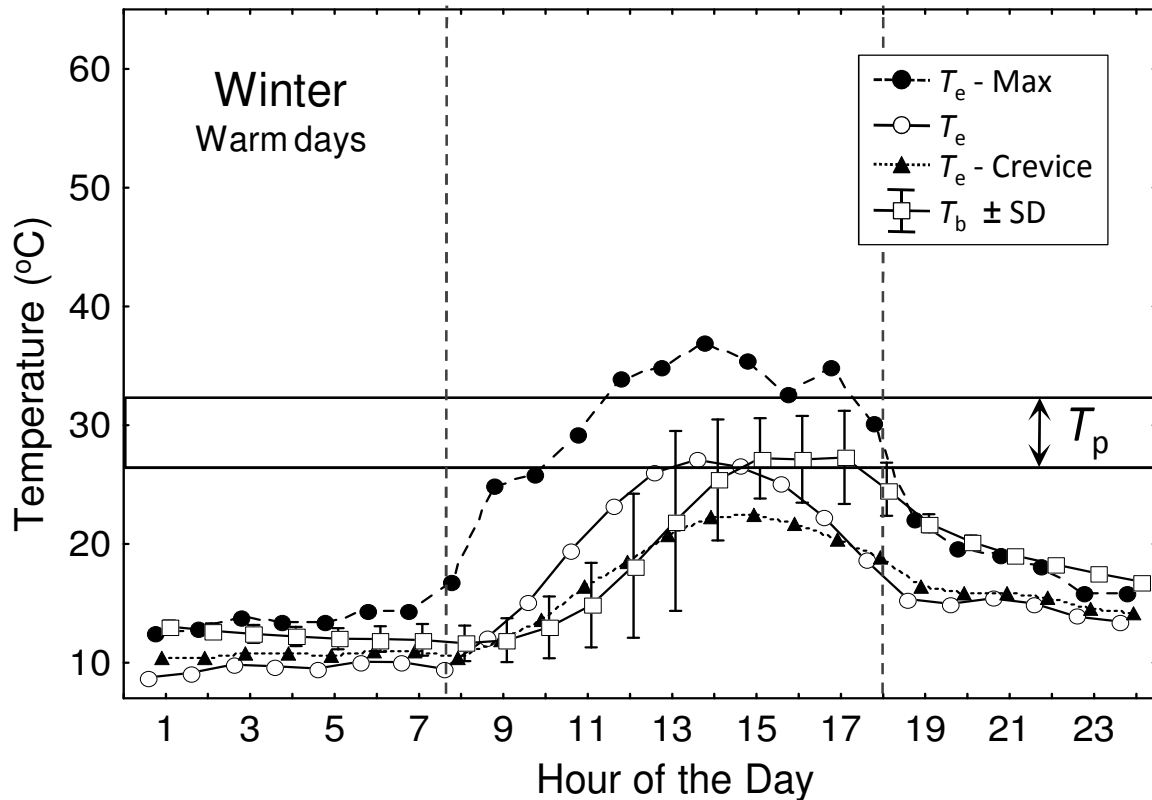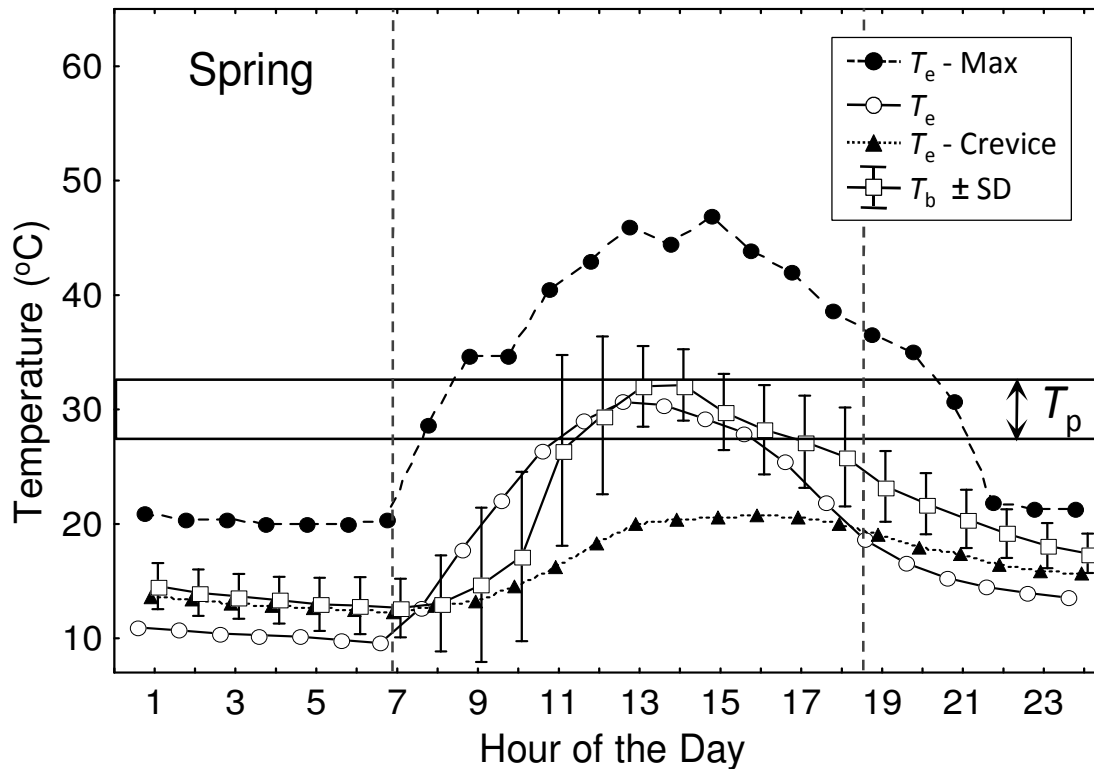
Figure 3.12. Hourly means of operative environmental temperatures (T_e), field body temperatures ($T_b \pm 1SD$) and crevice T_es, and the absolute maximum observed T_es (T_e-max) recorded in a coastal population of *C. cataphractus* during spring. The horizontal rectangle depicts the preferred temperature range (T_p) (an overlap with T_e indicating good thermal quality, $d_e = 0$). Vertical dotted lines indicate sunrise and sunset (South African Astronomical Observatory). Standard deviations are indicated only for T_b for clarity purposes (of the figure). The hourly means $\pm 1SD$ of T_e, T_e-crevice and T_b are given in Appendix Tables A3, A4 and A5.

Mean T_e varied significantly as a function of the distance from crevices ($F_{6,36} = 15.79$, $P = 0.01$), and when viewed graphically among time classes, variation was evident (Figure 3.6), further confirmed by a significant interaction between time of day (hour) and distance from crevice (hour*distance: $F_{6,36} = 15.79$, $P = 0.01$; Appendix Table A9). Mean T_es increased gradually up to 0.1 m from crevices, but then remained virtually invariable from 0.1 m to 0.9 m, generally being lower than T_p (Figure 3.6). During midday mean T_e increased

gradually as a function of distance from crevice, typically equalling T_p at the 0.1 m, 0.3 m and 0.9 m distance classes (Figure 3.9). In the afternoon, mean T_e was on average lower than T_p, yet nearly reaching T_p at the 0.3 m and 0.7 m distance classes (Figure 3.6). Only the mean T_es at the 0.5 m and 0.7 m distance classes differed significantly from crevice T_e ($P = 0.02$ and $P < 0.01$ respectively, Tukey-Kramer).

Mean T_es varied significantly among rock aspects representing the four wind directions ($F_{3,19} = 4.42$, $P = 0.02$; Figure 3.7), being highest and most favourable at the east facing aspects (Figure 3.7). Mean T_e at eastern aspects however differed significantly only from those recorded at western aspects ($P < 0.01$, Tukey-Kramer). Similarly, mean thermal habitat quality varied significantly among wind directions, being poor at the western aspects, with d_e being significantly higher than that of north- ($P < 0.01$, Tukey-Kramer), east- and south-facing aspects ($P < 0.01$, Tukey-Kramer) (Table 3.1). This geographical variation in both mean T_e and d_e was also a function of the time of day ($F_{11,209} = 224.74$, $P < 0.01$; Figure 3.7; Appendix Table A10).

3.4.2 Field body temperature (T_b), thermoregulatory accuracy (d_b), effectiveness of thermoregulation ($d_e – d_b$) and thermal exploitation (E_x)

3.4.2.1 Among-seasons comparison

Variation in mean field body temperatures (T_b), the average deviation of T_b from T_p (i.e. accuracy of thermoregulation, d_b) and the effectiveness of thermoregulation ($d_e – d_b$) were significantly affected by the time of day (i.e. hour), experimental day and season (Figures 3.13, 3.14 and 3.15; Appendix Table A11). When considered separately among seasons, mean field T_bs were significant lower in the winter period than summer, autumn and spring ($P < 0.01$, Tukey-Kramer). Moreover, mean T_b was significantly lower during the warm autumn than cooler spring ($P = 0.05$, Tukey-Kramer).
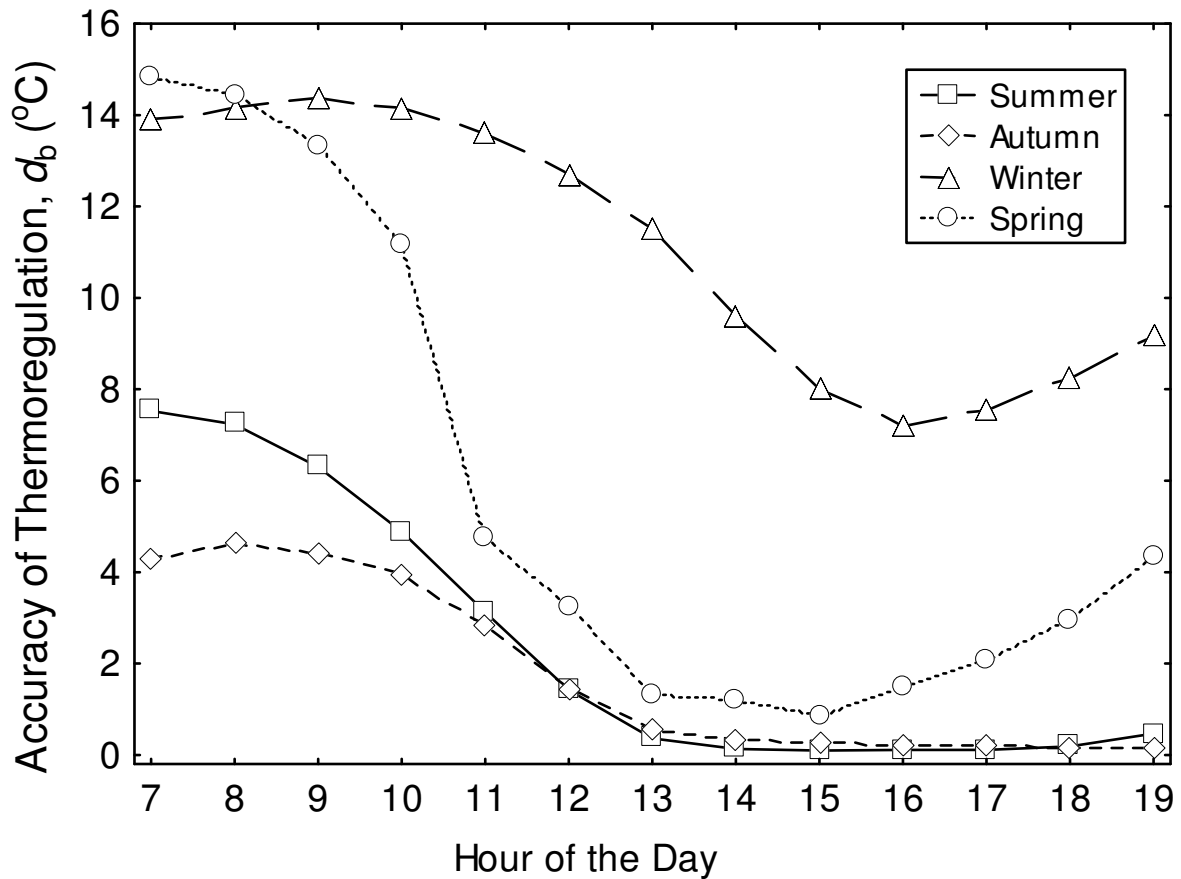
Figure 3.13. The accuracy of thermoregulation (d_b), observed in a coastal population of *C. cataphractus* as a function of the time of day. The accuracy of thermoregulation (d_b) is expressed as the degree of deviation between field body temperature (T_b) and T_p. A d_b value of zero indicates perfect accuracy (i.e. $T_b = T_p$) (Hertz *et al.* 1993). The hourly means ± 1SD of d_b is given in Appendix Table A6.
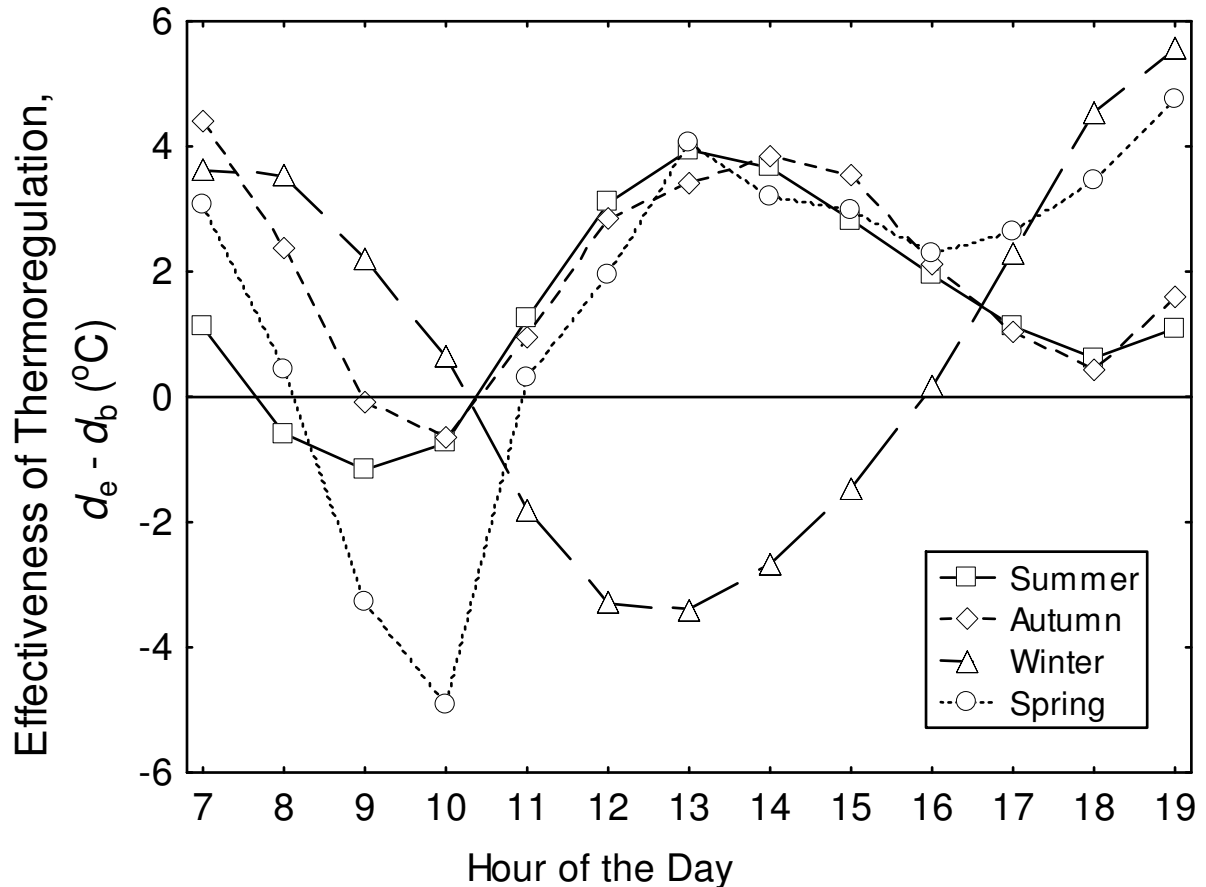
Figure 3.14. Effectiveness of thermoregulation ($d_e - d_b$) of a coastal population of *C. cataphractus* described as a function of time of day. The effectiveness of thermoregulation ($d_e - d_b$) expresses the degree of departure from thermoconformity ($d_e - d_b = 0$: perfect thermo conformity). Negative $d_e - d_b$ generally indicate the avoidance of thermally suitable microsites (Blouin-Demers and Weatherhead 2001). The hourly means ± 1SD of $d_e - d_b$ is given in Appendix Table A7.
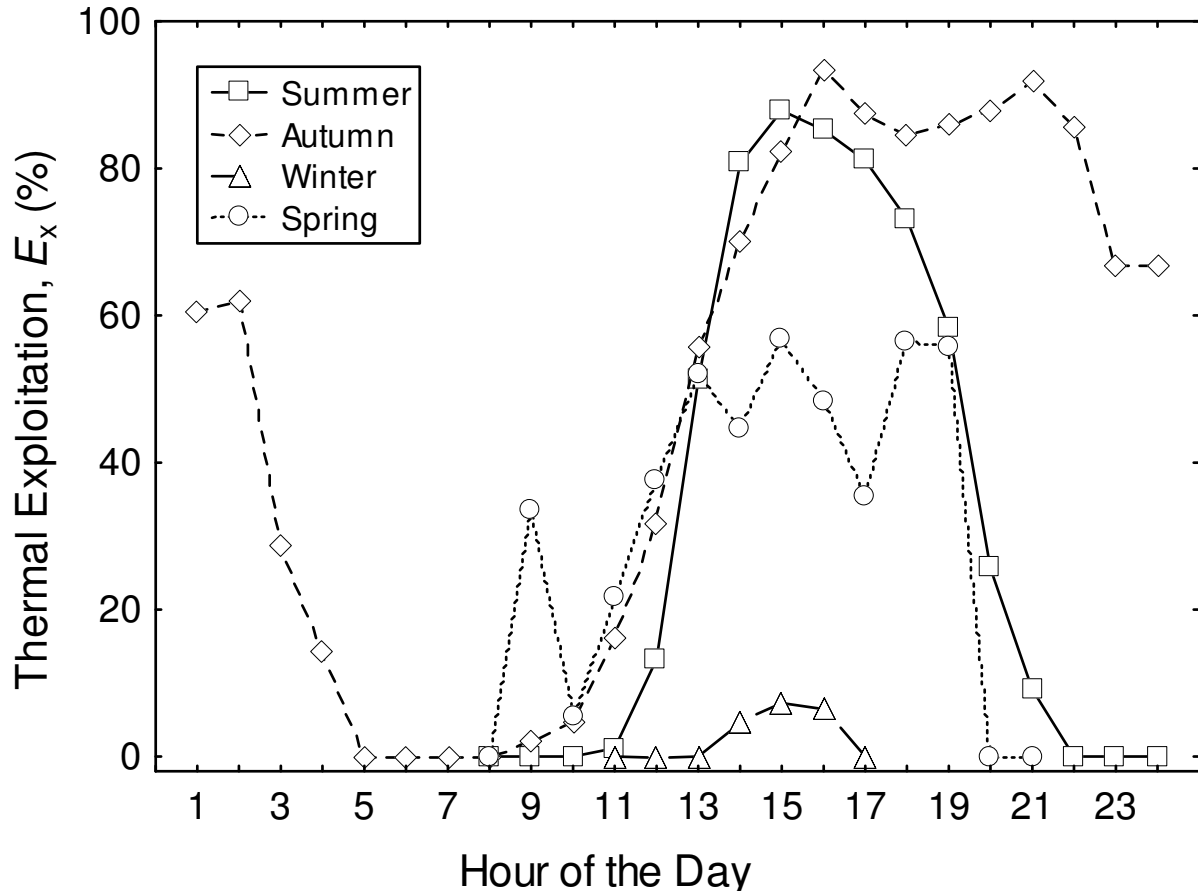
Figure 3.15. The thermal exploitation (E_x) of a coastal population of *C. cataphractus* described as a function of the time of day. Thermal exploitation describes the degree to which a reptile exploits the thermally favourable opportunities for precise thermoregulation, particularly describing the time-fraction (%) during which T_b equals T_p when permissive in a particular habitat (Christian and Weavers 1996). The hourly means ± 1SD of E_x is given in Appendix Table A8.

Lizards thermoregulated with the highest accuracy in autumn (i.e. low d_b); followed by summer, spring and least accurately during winter (Figure 3.13). Unlike T_b, these estimates of d_b differed significantly (pair-wise) among seasons (P < 0.01) except between summer and autumn ($P = 0.63$, Tukey-Kramer). The effectiveness of thermoregulation ($d_e - d_b$) was relatively invariable among summer, autumn and spring during most of activity time (11h00 – 16h00) (Figure 3.14). In contrast, during winter $d_e - d_b$ decreased below 0 ^{o}C during this period (11h00 – 16h00) (Figure 3.14). Lizards exploited their thermal habitat most proficiently during autumn, followed by summer, spring and winter respectively (Figure 3.15). When considered as a function of the time of day, thermal exploitation (E_x) was relatively invariable between summer and autumn from 14h00 to 17h00 (Figure 3.15).

3.4.2.2 Summer

Typical summer days

Mean field body temperatures (T_b) typically equalled T_p from 13h00 to 19h00 (overall mean: 25.8 ^{o}C ± 3.7 ^{o}C), being higher than crevice T_e throughout this period (Figure 3.3). The frequency distribution of T_b indicated a positive overlap between T_bs and T_p, in particular; 44.32 % of T_bs equalled T_p, 53.6 % were lower and only 2.1 % exceeded T_p (7h00 – 19h00) (Figure 3.16). Mean T_b did not vary significantly from both the crevice ($F_{1,29} = 0.22$, $P = 0.64$) and overall (in crevices and in the open) T_es ($F_{1,47} = 1.84$, $P = 0.18$) (7h00 – 19h00).

Although the average deviation of T_b from T_p (d_b, describing accuracy of thermoregulation) was moderate, being 3.7^{o}C ± 2.7^{o}C (7h00 – 19h00), lizards thermoregulated accurately from 13h00 to 19h00 (mean d_b < 1) (Figure 3.13).

The index for the effectiveness of thermoregulation ($d_e - d_b$) suggests active thermoregulation increased markedly from 11h00 and peaked at 13h00 (Figure 3.14). Lizards exploited their thermal habitat with moderate proficiency during summer (overall mean E_x = 53.2 % ± 35.5 %) (Figure 3.14), maintaining T_b within T_p 53.2 % of the time when permissive in their habitat (Figure 3.14). Mean thermal exploitation (E_x) increased rapidly after 12h00, peaked at 14h00, and then decreased rapidly from 19h00 (Figure 3.15).
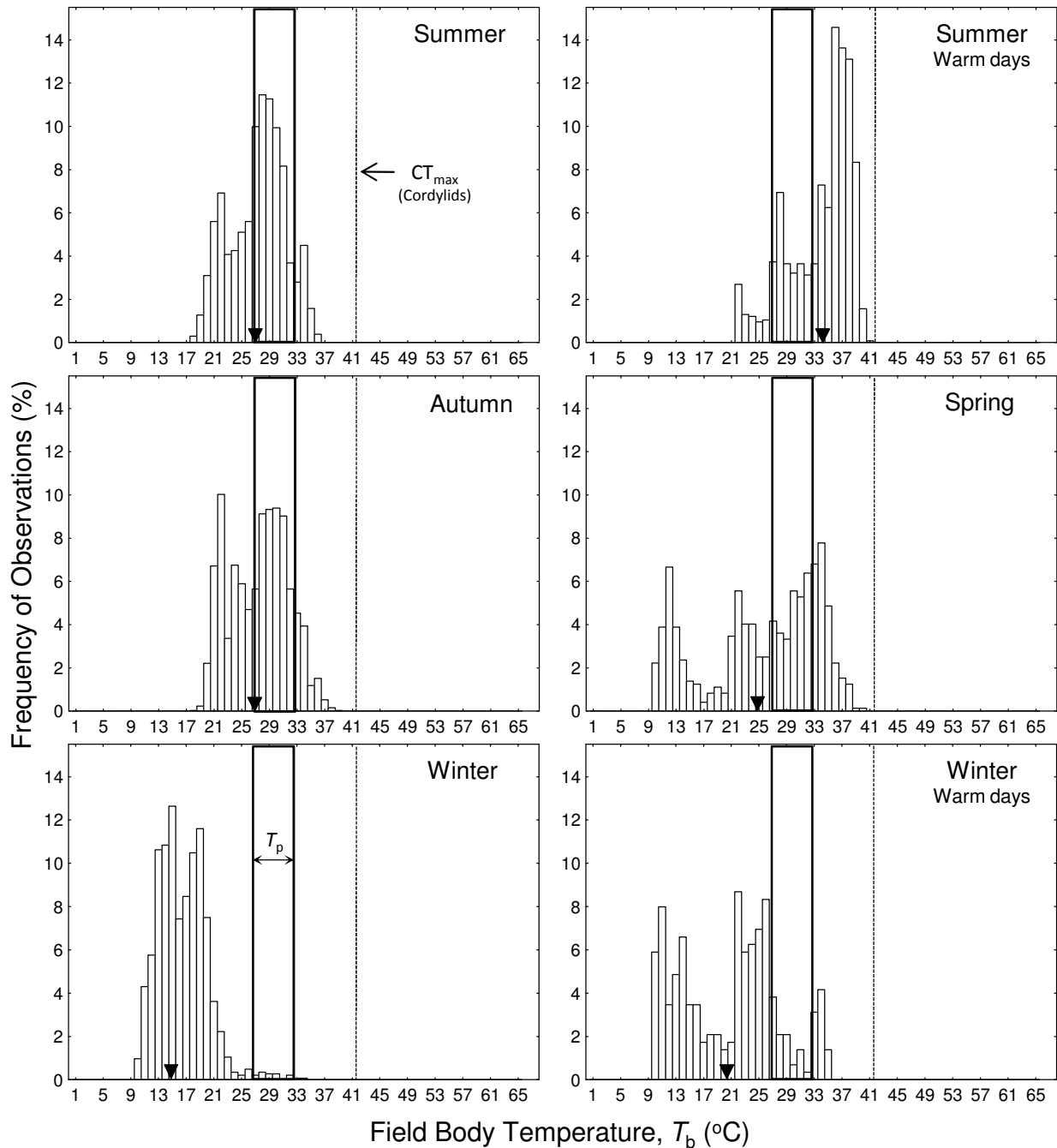
Figure 3.16. The frequency distributions of field body temperatures (T_b) recorded in a coastal population of *C. cataphractus* during summer, three abnormally warm summer days, autumn, spring, winter and two abnormally warm winter days (7h00 – 19h00). Arrow heads indicate overall mean T_b, whereas the vertical rectangle depicts the preferred temperature range (T_p) of *C. cataphractus* (N = six subjects in summer, seven in autumn, three in winter and three in spring). Vertical dotted lines indicate the mean CT_{max} known among cordylids to date (*C. niger*, *C. oelofseni*, *C. cordylus*: 41.5 °C (Clusella-Trullas *et al.* 2009)).

Exceptionally warm summer days

Lizards maintained high T_bs during the four hot summer days on average exceeding the upper bound of T_p (overall mean T_b = 33.4 ^{o}C ± 4.6 ^{o}C) (Figure 3.3). The lizards typically maintained T_bs within T_p only from 10h00 to 11h00, after which mean T_b increased, remaining above T_p from 12h00 to 21h00 and peaking at 16h00 (Figure 3.3). Mean T_b corresponded to mean crevice T_e from 13h00 to 7h00 (Figure 3.3). The maximum T_b measurement recorded in summer was 40.2 ^{o}C and not a single T_b measurement recorded between 14h00 and 19h00 was below the upper bound of T_p (i.e. 32.6 ^{o}C). The frequency distribution of T_b indicated a high degree of mismatch between T_b and T_p, in particular, 24.2 % of T_bs were within T_p, 10.9 % below, and 64.8 % above (7h00 − 19h00) (Figure 3.16). Mean T_b varied significantly from both the crevice T_es ($F_{1,48}$ = 4.49, P = 0.04) and overall T_es ($F_{1,22}$ = 97.37, P < 0.01) (7h00 − 19h00).

3.4.2.3 Autumn

Mean field body temperatures (T_b) remained near the preferred temperature range (T_p) during autumn (overall mean T_b = 27.0 ^{o}C ± 4.2 ^{o}C) and typically equalled T_p from 13h00 to 22h00, after which it gradually decreased until 9h00 (Figure 3.9). Mean T_bs closely matched crevice T_es from 9h00 to 17h00 (Figure 3.9). The frequency distribution of T_bs indicate a relatively good match with T_p, in particular, 50.2 % of T_bs equalled T_p, 42.4 % were lower and 7.37 % higher than T_p (7h00 − 19h00) (Figure 3.11). Mean T_b varied significantly from both the crevice ($F_{1,12}$ = 1.18, P = 0.23) and overall T_es ($F_{1,26}$ = 3.78, P = 0.06) (7h00 − 19h00).

Lizards in general thermoregulated accurately in autumn (overall mean d_b = 1.6 ^{o}C ± 2.2 ^{o}C), and foremost so from 13h00 to 23h00 (d_b < 1) (Figure 3.13). The effectiveness of thermoregulation ($d_e − d_b$) was moderate in autumn (Figure 3.14). In particular, mean $d_e − d_b$ values decreased slightly below zero from 9h00 to 10h00 after which it increased, peaking at 14h00, and then declined again gradually until 18h00 (Figure 3.14). Lizards exploited their thermal habitat with relatively high proficiency in autumn (overall mean E_x = 58.5 % ± 33.8 %) (Figure 3.14), maintaining T_b within T_p 58.5 % of the time when it was permissive in their habitat (Figure 3.14).

3.4.2.4 Winter

Normal winter days

Field body temperatures were low during winter (overall mean T_b = 16.0 ^{o}C ± 3.4 ^{o}C), following the trend observed in T_e (Figure 3.10). Mean T_bs closely corresponded to mean crevice T_es from 9h00 to 13h00, and then exceeded it for the remainder of the day (Figure 3.10). The frequency distribution of T_bs indicate an almost total mismatch with T_p, in particular, only 1.2 % of T_bs were within T_p, 98.8 % below, and 0.1 % above (7h00 – 19h00) (Figure 3.16). Body temperatures did not vary significantly from crevice T_e (P = 0.14, $F_{1,7}$ = 2.84) (7h00 – 19h00).

Lizards thermoregulated with low accuracy during winter (overall mean d_b = 10.9 ^{o}C ± 3.3 ^{o}C), and although accuracy increased gradually from 9h00, on average, it remained low throughout the day (Figure 3.13). The effectiveness of thermoregulation (d_e – d_b) was also low and decreased below zero for the majority of activity time (10h00 – 15h00) (Figure 3.14). Lizards exploited their thermal habitat with poor proficiency and mean E_x values were below 10 % throughout the day (overall mean E_x = 2.6 % ± 3.3 %) (Figure 3.15).

Warm winter days

Unlike the colder days, mean T_bs indeed equalled T_p for a portion of the day (15h00 – 17h00) during the two abnormally warm winter days, and exceeded mean crevice T_es for most of activity time (13h00 – 19h00) (Figures 3.11 and 3.17). Of the T_bs observed from 7h00 to 19h00, 9.7 % equalled T_p, 5.6 % were higher and 84.7 % lower than T_p (7h00 – 19h00) (Figure 3.16).

The lizards thermoregulated with low accuracy during the warm winter days (overall mean d_b: 7.2 ^{o}C ± 6.0 ^{o}C), yet maintained a high effectiveness of thermoregulation suggesting active thermoregulation (overall mean d_e – d_b: 7.2 ^{o}C ± 6.0 ^{o}C). Lizards exploited their thermal habitat with low proficiency (overall mean 18.4 % ± 22.2 %).
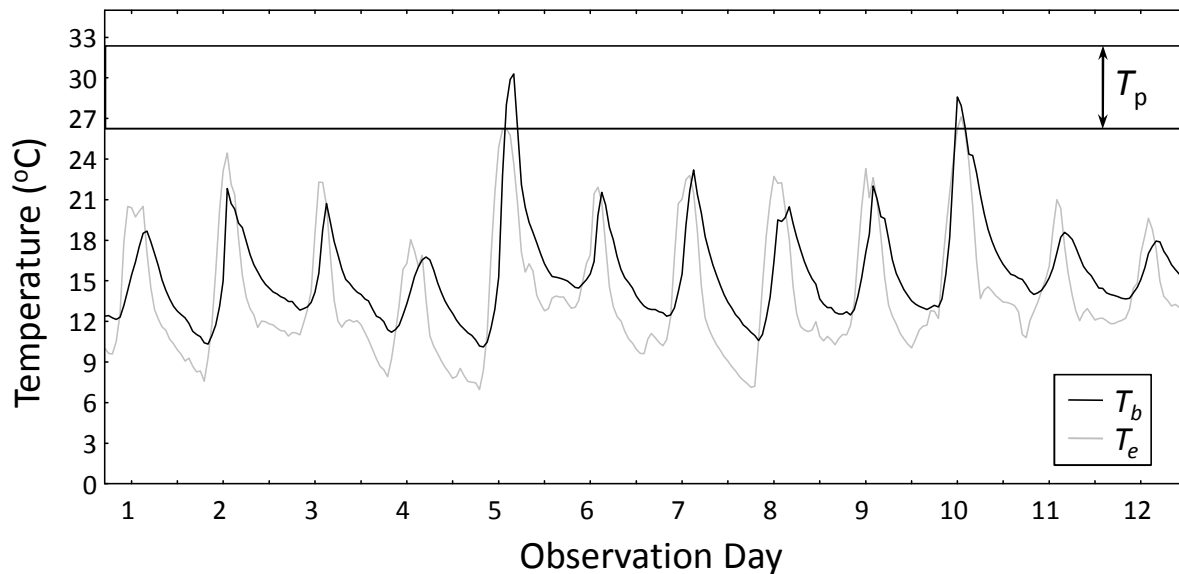
Figure 3.17. Operative environmental temperature (T_e) and field body temperature (T_b) recorded at 15 minute intervals across 12 winter days in a coastal population of *C. cataphractus.* The horizontal rectangle depicts the preferred temperature range (T_p) of *C. cataphractus.*

3.4.2.5 Spring

Field body temperatures (T_b) corresponded moderately to T_p during spring, on average being slightly below T_p (overall mean T_b = 24.9 ^{o}C ± 8.2 ^{o}C) (Figure 3.12). Mean T_bs increased gradually from 8h00, peaking at 13h00 and then declined again until 7h00, on average equalling T_p from 12h00 to 16h00 (Figure 3.12). The frequency distribution of T_bs indicates a moderate match with T_p, and a high frequency of T_bs below T_p, in particular, 29.4 % of T_bs were within T_p, 52.6 % below, and 17.9 % above (7h00 – 19h00) (Figure 3.16). Mean T_bs varied significantly from mean crevice T_es ($F_{1,8}$ = 14.62, P = 0.01), but not from overall (in crevices and in the open) mean T_es ($F_{1,29}$ = 0.06, P = 0.81) (7h00 – 19h00).

Lizards thermoregulated with relatively low accuracy during spring (overall mean d_b = 5.1 ^{o}C ± 5.9 ^{o}C). The hourly pattern of thermoregulatory accuracy however indicates a relatively low deviation of T_b from T_p (i.e. high accuracy) between 13h00 and 16h00 (d_b < 2 ^{o}C) (Figure 3.13). The effectiveness of thermoregulation (d_e – d_b) was moderate, yet decreased to below zero from 9h00 to 10h00, after which it increased rapidly, peaking at

13h00 (Figure 3.14). Lizards exploited the thermal habitat with moderate efficiency in spring (overall mean E_x = 39.7 % ± 18.6 %), mean E_x being highest from 13h00 to 19h00 (Figure 3.15).

3.5 Discussion

Cordylus cataphractus exhibits the lowest T_p observed among cordylids to date (Chapter 2). Thermal preference was estimated in two populations of *C. cataphractus* and was found to be conserved among the dry warm autumn and cooler more mesic spring, suggesting the absence of seasonal plasticity in T_p (Chapter 2). Seasonal variation in the thermal habitat and high temperatures will therefore create challenges to *C. cataphractus*, possibly constraining surface activity as well as time and energy budgets of individuals at certain times of the year due to altered T_b and thermoregulatory requirements (Blouin-Demers and Weatherhead 2001).

The current results indicate that the quality of the thermal habitat of *C. cataphractus* varies significantly at micro and macro temporal scales (i.e. across days and among seasons) as well as at micro spatial scale (around rocks). Thermoregulatory indices (i.e. d_b, $d_e - d_b$ and E_x) (Hertz *et al.* 1993; Christian and Weavers 1996; Blouin-Demers and Nadeau 2005) suggest that *C. cataphractus* responds to seasonal T_e flux by actively regulating T_bs (i.e. thermoregulation) during summer, autumn and spring. The current results further suggest a correlation between surface activity (microhabitat selection) patterns known for *C. cataphractus* and the general distribution of thermally favourable microhabitats (high thermal quality) during autumn and spring.

The quality of the thermal habitat (d_e) of *C. cataphractus* (i.e. absolute deviation of T_e from T_p) varied seasonally being most favourable during autumn, followed by summer, spring and winter respectively. Micro-scale variation in thermal quality varied significantly as a function of distance from crevice edge during all seasons but winter. This variation was linked to the time of day, as expected due to solar movement, in combination with the subsequent gradual heating and cooling of rocks as a source of reradiated IR (Bakken and Gates 1975; Huey *et al.* 1989). The spatial variation in T_e showed that individuals could attain T_b within T_p through microsite selection for the majority of the day during summer and autumn, whereas in spring this was only possible after 11h00 and in winter a very limited proportion of T_es within T_p were documented. However, during two warmer winter days,

favourable thermal conditions (T_es within T_p) and basking spots were available at certain times, therefore allowing accurate thermoregulation.

To assess microsite-level variation in the thermal habitat of *C. cataphractus*, different subsets of T_e-models were spread among rock aspects representing the four major wind directions. Operative environmental temperatures and the resulting thermal habitat quality (d_e) varied significantly among the four wind directions during summer, autumn and spring. East was warmest and most favourable during the colder winter and spring periods, whereas south was most favourable during the warmer summer and autumn periods. The variation in T_e among directions was also a function of time of day during each season as expected due to solar cycles in combination with the subsequent gradual heating and cooling of rocks as a source of radiated IR (Huey *et al.* 1989).

Seasonal patterns of retreat-site selection have been coupled with thermal characteristics of rocks in various reptiles, particularly enabling individuals to maintain T_bs within their preferred temperature ranges (Webb and Shine 1998; Kearney and Predavec 2000; Kearney 2002; Shah *et al.* 2004). Webb and Shine (1998) described the thermal habitat of *Hoplocephalus bungaroides*, and by assuming that snakes would select T_e within their T_p, Webb and Shine (1998) predicted seasonal patterns of habitat use. Webb and Shine (1998) then confirmed their predictions with mark recapture data and field body temperature measurements. During spring, these authors found that individuals actively selected small or thin unshaded rocks and used these "hot" rocks to maintain T_b within T_p, and further that individuals selected crevices exposed to the afternoon sun, avoiding easterly and southerly crevices that were generally cooler. Similarly, seasonal patterns of retreat-site selection may vary in *C. cataphractus* since these lizards have been reported to remain within crevices for prolonged periods (Visagie 2001). In particular, the significant variation of thermal habitat quality around rocks currently observed indicates that seasonal shifts in retreat-sites around large rocks will be beneficial. Moreover, the current data predict that *C. cataphractus* individuals will preferentially be present at eastern aspects of rocks during the

cooler spring and winter months and at southern aspects during the warmer summer and autumn periods.

Hayward (2008) surveyed 131 *C. cataphractus* groups during the warm dry summer months across three localities in the Lamberts Bay - Graafwater district (approximately 80km north-east of the current study site) and found that the majority of groups inhabited north-westerly to westerly facing crevices. Although the current results indicate south as thermally most favourable during summer, northern and western aspects also had markedly higher thermal quality than east suggesting that thermal factors may have played a role in the microhabitat selection of the population described by Hayward (2008).

The selective utilization of favourable retreat sites around rocks is however complicated by the group-living life strategy. In particular, free standing rocks, including crevices on all four aspects of the rock, may house *C. cataphractus* groups of up to 58 individuals (Effenberger and Mouton 2007). The males are highly territorial, and maintain neighbouring territories of approximately ~0.79 m^2, which they aggressively defend (Effenberger and Mouton 2007). The observed variation in thermal habitat quality around rocks may therefore provide an incentive for intra-group male-male competition to secure favourable microsites, due to the direct relationship between thermal habitat quality and reptile time and energy budgets (Huey and Slatkin 1976; Gvozdik 2002). The cost associated with obtaining an optimal basking site may therefore be higher than when using the optimal basking site when solitary. Unlike males, females move freely around rocks during the mating season (Effenberger and Mouton 2007) and are thus expected to position themselves within microsites of superior thermal quality. Males inhabiting territories of high (thermal) quality may therefore attain the additional benefit of increased female access.

Competition for suitable basking sites has been reported in several reptiles (Huey 1982; Phillips *et al.* 1993; Seebacher and Grigg 1997; Seebacher and Grigg 2001; Angilletta 2009). For example, Seebacher and Grigg (2001) found that dominant crocodiles chase subordinates from thermally favourable basking sites. An exploration of the relationship between thermal habitat quality around rocks and male dominance structure may provide

support for the prevalence of competition for thermal habitats in *C. cataphractus*. On the other hand, variation in d_e around rocks may stagger individuals temporally and spatially, resulting in differential activity patterns around the rock limiting the possible competition for best basking sites or vantage points for potential prey inherent to large social groups. Effenberger and Mouton (2007) did not mention the possibility of temporal variation in activity patterns around the rock and further investigation is needed.

The reduced surface activity reported for *Cordylus cataphractus* extends throughout the dry late summer, autumn and cooler winter months (Visagie 2001). During these periods, individuals predominantly remain within crevices, often basking with only their heads protruding and occasionally emerging to within 0.1 m from crevices (Visagie 2001; Hayward 2008). Conversely, these lizards are fully active outside on rock surfaces during spring and frequently move up to 0.9 m from crevices (Visagie 2001; Effenberger and Mouton 2007), actively basking and foraging (Effenberger 2004). Although thermal habitat quality was highest at eastern aspects of rock habitats during spring, it was least favourable in summer and autumn due to high T_es and males may therefore benefit from altering territory boundaries (around rocks) according to varied thermal quality among seasons. Territoriality has however only been studied during spring which marks the peak mating season (Effenberger and Mouton 2007). It may be that territoriality diminishes during the rest of the year when the surface activity of *C. cataphractus* is repressed, causing males to remain in the close proximity of each other beneath and on the edges of rocks.

Mean field body temperatures (T_b) varied significantly at seasonal scale being highest in autumn, followed by summer, spring and winter respectively. Literature records of T_b are generally limited for the Cordylidae family, available only for summer and winter (Table 3.2) (Bowker 1984; Bauwens *et al.* 1999; Lailvaux *et al.* 2003; Clusella-Trullas *et al.* 2009; McConnachie *et al.* 2009). The summer mean T_b observed for *C. cataphractus* is the lowest observed among cordylids (Table 2). The low summer mean T_b is expected since *C. cataphractus* exhibits the lowest preferred temperature range (T_p) recorded among cordylids to date (Chapter 2). The low T_p and subsequently low T_bs (currently observed) may be a

mechanism of energy conservation through the associated decrease in metabolic expenditure (Shine and Lambeck 1990; Christian and Bedford 1995). *Cordylus cataphractus* however exhibits a resting metabolic rate (RMR) 68 % lower than that reported for any other cordylid to date (at corresponding T_as), being relatively constant between T_as of 10°C, 15°C, 20 ^{o}C, 25 ^{o}C and 30 ^{o}C (Mouton *et al.* 2000b), suggesting that basal energy expenditure will be less influenced by lowered T_b and that the lowered T_p and T_b likely is the result of other factors (discussed later) (Chapter 2). Although T_p was shown to be low and did not vary significantly among seasons, the potential of lowered T_p targeted at energy conservation cannot be discounted, particularly, since T_p was found to be consistently lower during the warmer dry autumn than cooler more mesic spring (although not significantly so) (Chapter 2).

Table 3.2. Daily mean field body temperatures (T_b) recorded among cordylids to date.

Species	Season				Reference
	Summer	Autumn	Winter	Spring	
Platysaurus intermedius w.	28.8	-	-	-	Lailvaux *et al.* 2003
Cordylus macropholis	28.9	-	-	-	Bauwens *et al.* 1999
Pseudocordylus m. melanotus	28.9	-	26.3	-	McConnachie *et al.* 2009
Gerrhosaurus major	34.5	-	-	-	Bowker 1984
Gerrhosaurus nigrolineatus	35.2	-	-	-	Bowker 1984
Gerrhosaurus flavigularis	33.8	-	-	-	Bowker 1984
Cordylus cataphractus	25.8*	27.0	16.0	24.9	Current study
Cordylus oelofseni	28.7	-	12.5	-	Clusella-Trullas *et al.* 2009
Cordylus niger	27.1	-	20.1	-	Clusella-Trullas *et al.* 2009
Cordylus cordylus	27.8	-	20.5	-	Clusella-Trullas *et al.* 2009

*Typical summer days (N = 11days).

Clusella-Trullas *et al.* (2009) assessed thermoregulation in three cordylid species (*C. cordylus*; *C. niger*; *C. oelofseni*) and found that although their habitats provided a wide array of T_es in summer, the T_bs recorded in the field were often below the lower boundary of T_p. In contrast, the current results indicated that *C. cataphractus* tolerated T_bs exceeding T_p during

activity time in spring, whereas T_bs were typically maintained within T_p during summer and autumn. Clusella-Trullas *et al.* (2009) suggested the T_b-T_p mismatch to be either due to active avoidance of warmer T_es, therefore functioning to reduce overheating risk, or due to the compromise between general behaviour such as mating, feeding, maintaining territories and thermoregulatory investment (i.e. the thermoregulatory cost-benefit ratio operational in these species) (Huey and Slatkin 1976). Alternatively, seeing that the trend of T_b-T_p mismatch was consistent in all three species observed by Clusella-Trullas *et al.* (2009), it may have been the result of an overestimate of T_p. The T_ps of all three species were estimated in photothermal gradients which lacked retreat sites (Clusella-Trullas *et al.* 2007), even though these species are known to rely primarily on crevices as anti-predatory mechanism (Losos *et al.* 2002). Conversely, the T_p of *C. cataphractus* was estimated in photothermal gradients containing crevices, possibly providing a more realistic estimate of T_p (see Chapter 2), but also with the possibility of resulting in a lower T_p.

The absolute deviation of T_b from T_p (d_b) (i.e. thermoregulatory accuracy, where a low d_b indicates high accuracy) varied proportional to thermal habitat quality (i.e. autumn < summer < spring < winter). Seasonal variation in the absolute deviation of T_b from the target T_p (d_b) is common among squamate species (Huey *et al.* 1977; Avery 1982; Hertz 1992; Kearney and Predavec 2000; Clusella-Trullas *et al.* 2009; McConnachie *et al.* 2009). Such variation in d_b may be a result of seasonal variation in T_e and the associated cost-benefit balance related to the interplay of food resource availability and suitable thermal opportunities (Huey and Slatkin 1976; Pyke *et al.* 1977; Huey and Pianka 1981), in combination with other factors such as predation risk (Downes 2001; Herczeg *et al.* 2008) and social behaviour (Dewitt 1967; Labra 1995). The current daily pattern of the effectiveness of thermoregulation (i.e. departure from conformity, $d_e - d_b$) was relatively conserved among summer, autumn and spring suggesting uniform investment among these seasons. This suggests that although *C. cataphractus* may perform active thermoregulation, the cost of thermoregulation is moderate and that the seasonal d_b shifts are passive (i.e. thermoregulatory investment corresponds among seasons), occurring proportionate to

changes in thermal habitat quality (d_e) (Kearney and Predavec 2000). In a study on the permanent aggregating *Cordylus macropholis*, Bauwens *et al.* (1999) reported a mean T_b of 28.4 °C for individuals caught within *Euphorbia caput-medusae* plants and 29.4 °C for individuals on the outside surface branches of the same plant during summer. The authors reported the absence of basking behaviour and suggested that *C. macropholis* does not perform overt thermoregulatory behaviour, but rather, simply thermoconforms to thermal conditions within *E. caput-medusae* plants. In contrast, the current results show that *C. cataphractus*, as other members of Cordylidae (of which records exist), perform active behavioural thermoregulation (Clusella-Trullas *et al.* 2009; McConnachie *et al.* 2009).

Regions hosting *C. cataphractus* are characterised by sparse vegetation cover and low insect abundance during the dry season (i.e. summer and autumn) (Hayward 2008). The low food availability is expected to affect individuals living in groups (such as *C. cataphractus*) more than other solitary-living species. In fact, confirming this, Mouton *et al.* (2000a) found that 63.7 % of *C. cataphractus* individuals captured during autumn had empty stomachs ($N = 91$). Lizards are expected to remain inactive when the energy gained through activity does not outweigh the costs of being active (as stated by the optimal foraging theory) (Huey and Slatkin 1976; Pyke *et al.* 1977; Pough 1980), and it is therefore not surprising that other researchers have attributed the lowered surface activity of *C. cataphractus* and tendency to remain in crevices during the dry season to food constraints related to group-living (Visagie 2001; Hayward 2008). The solitary-living *Cordylus polyzonus* that in many cases share rock outcrops and even crevices with *C. cataphractus* (personal observation) remains active throughout the year and frequently moves away from crevices during the dry warm periods (Visagie 2001; Hayward 2008), supporting the notion that seasonal repressed activity in *C. cataphractus* is related to permanent group-living in an arid context (Visagie 2001; Hayward 2008). The mean T_p reported for *C. polyzonus* however is 3.8 °C higher than that of *C. cataphractus* (Clusella-Trullas *et al.* 2007; Chapter 2), and the lower surface activity of *C. cataphractus* during the warm summer and autumn months (compared to *C. polyzonus*) may therefore be associated with thermal preference, since mean T_es in the open are typically

high at the time. *Cordylus polyzonus* have much thinner dermal armature than *C. cataphractus* (Loveridge 1944), therefore being more manoeuvrable, which, together with the different life strategy employed (i.e. solitary-living versus group-living), is expected to result in considerably different cost-benefit balances in regard to activity (and therefore thermoregulation) than *C. cataphractus*. The field thermal ecology of *C. polyzonus* currently remains unexplored and such investigation will be profitable and may aid interpreting the effect of group-living in *C. cataphractus* on thermoregulation since these lizards occur in sympatry.

The micro-spatial variation of T_e during autumn (i.e. dry season) indicates that individuals could maintain T_b within T_p for the majority of the day when present on the edges of or within crevices. Theoretically, microsite selection (e.g. remaining within crevices) represents a mode of behavioural thermoregulation, incurring a (foraging) time-cost to the animal (Huey 1982; Kearney and Predavec 2000), and the repressed surface activity observed in *C. cataphractus* during autumn (Visagie 2001) may therefore occur actively for thermoregulatory purposes. Operative environmental temperatures (T_e) exceeded T_p in the open for a large part of activity time during autumn thus indicating the need for shuttling and/or precise microsite selection to maintain T_b near T_p (Bauwens *et al.* 1996; Diaz and Cabezas-Diaz 2004). Foraging is however unlikely to compensate for the cost associated with such active behavioural thermoregulation because of the resource (food) limitation at the time (Mouton *et al.* 2000a), and lowered surface activity is expected (Pyke *et al.* 1977; Pough 1980), yet, likely being the result of resource limitation (Visagie 2001; Hayward 2008) in combination with thermal constraints (Grant and Dunham 1988).

Certain lizard species are known to regulate body temperatures whilst in crevices (outside of direct solar radiation) and may even do so more effectively than in the open (Cowles and Bogert 1944; Huey 1982). Thermoregulation within retreats is generally achieved behaviourally through microsite selection (Lemos-Espinal *et al.* 1998; Kearney 2002), postural adjustments which alter surface contact (Cowles and Bogert 1944; Huey 1982) and social huddling (Lanham 2001; Shah *et al.* 2003). Although T_e-models were

placed beneath rocks during all four seasons, a detailed exploration of crevice thermal habitats was only performed in summer (27 T_e-models). These crevice T_es varied significantly beneath rocks as a function of rock thickness, crevice height and distance from crevice edge, indicating the potential for behavioural thermoregulation in crevices. Individuals inhabiting large rocks may therefore gain benefit during warm periods since a wide array of thermal opportunities is provided. *Cordylus cataphractus* individuals housed in laboratory photothermal gradients fitted with crevices in the cool sections were found to emerge from crevices and exploit heat sources more than 0.5 m away in order to increase T_b (i.e. thermoregulate) during autumn (Chapter 2). This suggests that *C. cataphractus* performs active thermoregulation in the field during autumn and will if needed move from crevices to basking sites when temperatures are unfavourable inside. Behavioural thermoregulation (through microsite selection and postural adjustments) is therefore likely to occur beneath rocks. In fact, a time-based focal scan (Altmann 1974) on *C. cataphractus* performed during autumn (a single day) indicated that certain individuals alter their body postures (relative to rock surfaces) whilst in crevices (section 3.3.4). The active behavioural thermoregulation observed in autumn further supports the notion that the lowered surface activity reported for *C. cataphractus* at the time (Visagie 2001) is related to the thermal environment. *Cordylus cataphractus* has heavy dermal armature which provides protection against terrestrial predators, however, being less effective against birds of prey (Hayward 2008). Armour may permit lizards to use habitats and behaviours that are too dangerous for unarmoured species (Losos *et al.* 2002). In *C. cataphractus*, the heavy armature may allow individuals to exploit the wider sections of crevices (that are accessible to terrestrial predators) and therefore varied thermal opportunities beneath rocks for thermoregulatory purposes, which other cordylids likely will not be able to do.

In summer, thermal habitat quality was higher in the open than inside crevices, and the hourly variation in mean T_e indicates that emergence behaviour will be beneficial at the time. In fact, mean T_b exceeded crevice T_e from 13h00 to 19h00 suggesting that lizards indeed emerged from crevices. Visagie (2001) reported repressed surface activity in *C.*

cataphractus from February to April. The sampling in the current study for summer occurred during January and suggests *C. cataphractus* indeed emerges consistently from crevices during this period. Focal observations are however needed to confirm emergence behaviour.

During spring, when *C. cataphractus* is known to spend the majority of the day outside of crevices (Effenberger and Mouton 2007), thermally suitable opportunities were recorded exclusively at microsites outside of crevices during midday and lizards evidently had to emerge from crevices throughout the day in order to attain T_b near T_p. Spring is also the period when ample food (invertebrates) is available outside of crevices (Struck 1994) as well as the peak mating season of *C. cataphractus* (Flemming and Mouton 2002), therefore further motivating emergence behaviour. The frequency distribution of T_es available in spring indicates a relatively normal spread above and below T_p, and T_es of up to 45 ^{o}C were present. Lizards therefore would have had to thermoregulate behaviourally (cost incurred) to not overheat, at least at certain times.

In winter when *C. cataphractus* reportedly exhibit lowered surface activity (Visagie 2001), mean T_es were generally unfavourable (i.e. lower than T_p) both within and outside of crevices. Lizards are known to remain inactive when T_es within T_p are unavailable (in accordance with the cost-benefit model of thermoregulation) (Huey and Slatkin 1976; Herczeg *et al.* 2006; Herczeg *et al.* 2008) and the repressed activity of *C. cataphractus* observed during winter (Visagie 2001) is therefore as expected from a thermal perspective. Certain reptiles are however known to be active in spite of unfavourable thermal conditions in order to gain some foraging benefit (Blouin-Demers and Weatherhead 2001), and repressed activity can therefore not implicitly be linked to cool temperatures in *C. cataphractus*.

Although winter was characterized by low unfavourable T_es, mean T_e indeed reached T_p for a portion of the day during two abnormally warm winter days and lizards responded by actively thermoregulating, maintaining mean T_b within T_p for at least three hours per day. The mean deviation of T_b from T_p (accuracy of thermoregulation) was 7.2 ± 6.0^{o}C, in comparison to the 10.9 ^{o}C ± 3.3 ^{o}C observed on the typical winter days, suggesting that the

repressed activity observed during winter is indeed related to suboptimal environmental temperatures and that *C. cataphractus* utilizes windows of thermally suitable conditions as has been described in other cordylids (Clusella-Trullas *et al.* 2009). Shuttleworth *et al.* (2008) collected *C. cataphractus* scats during each month of the year and found that the proportion of termite heads in scats were highest during mid-winter (June to July) (~33%). The warm days may therefore be essential for the prevalence of termitophagy during winter, firstly, permitting both lizard and termite activity (Arab *et al.* 2005), and secondly providing suitable temperatures for lizards to digest ingested termites (Stevenson *et al.* 1985; Van Damme *et al.* 1991; Zhang and Ji 2004). Warmer winter days may also benefit vitellogenesis (Licht 1972) which occurs throughout winter in *C. cataphractus* (Flemming and Mouton 2002).

Seasonal activity patterns of lizards are generally associated with resource availability and the associated cost-benefit balance (Huey and Slatkin 1976; Pyke *et al.* 1977; Davis and DeNardo 2010) and/or thermal regimes (Huey 1982; Grant and Dunham 1988), whereas other factors such as circadian cycles (Winne and Keck 2004), dehydration (Porter *et al.* 1973), satiation (Hardy 1962), predation (McFarland 1976) or foraging behaviour related to varied prey preference (Huey and Pianka 1981) may also have an effect. Although the current results show that environmental temperatures may influence the seasonal activity patterns of *C. cataphractus*, it is unlikely to be the principle determinant thereof.

Heavy dermal armature and subsequent low manoeuvrability/mobility suggests that predation is a major risk to *C. cataphractus* on outside surfaces (Losos *et al.* 2002; Hayward 2008). Predation risk by birds of prey is therefore a further probable contributor to the seasonal surface movement patterns of *C. cataphractus*, since the time spent near and within crevices is expected to be maximized.

The fact that *C. cataphractus* acts as a strict sit-and-wait forager (Mouton *et al.* 1999), yet also exhibits termitophagy (Shuttleworth *et al.* 2008), may also contribute to seasonal movement patterns (Huey and Pianka 1981). Shuttleworth (2006) surveyed 11 populations and never found a termite foraging port within four meters from a *C. cataphractus* crevice,

suggesting that these lizards do not rely on visual cues to locate ports, and that emergence from crevices will not necessarily aid termitophagy. The fact that *C. cataphractus* is known to emerge from crevices during spring and early summer (Effenberger and Mouton 2007) when insect abundance peaks (Struck 1994), yet remain close to, or within crevices during the dry mid to late summer and cold winter months (Visagie 2001) may be due to the increased reliance on termites during the last mentioned periods (Shuttleworth *et al.* 2008).

Operative environmental temperatures were cooler and less favourable outside of crevices at night during all seasons. Interestingly, mean T_bs were higher and nearer to T_p than mean crevice T_es throughout the night during autumn, winter and spring, suggesting active thermoregulation within crevices, possibly through microsite selection. During typical and warmer winter days, mean T_bs exceeded the maximum recorded T_e between 20h00 and 22h00. Optimal T_bs at night may benefit physiological processes such as vitellogenesis and spermatogenesis (Licht 1972) or aid digestion (Van Damme *et al.* 1991), which may benefit *C. cataphractus* during spring when food abundance is high and fat reserves need to be deposited (Flemming and Mouton 2002).

Social aggregation in reptiles is often associated with thermoregulation (during cold conditions) (Boersma 1982; Lanham 2001; Shah *et al.* 2003). Shah *et al.* (2003) found that social aggregating gecko, *Nephrurus milii*, huddled closer together when T_es were lowered, and that huddled individuals heated and cooled slower than solitary ones. The authors suggested that thermoregulation is the primary drive force for sociality in *N. milii*. Similarly, the skink *Egernia stokesii* is known to form aggregations during cooler conditions, enabling individuals to retain body heat for longer (than those occurring solitarily) (Lanham 2001). The fact that T_bs exceeded the maximum T_es observed between 20h00 and 22h00 and mean crevice T_e throughout the night during both typical and the warmer winter days suggests that huddling behaviour (rather than microsite selection or postural adjustments) may be a real possibility during those periods, worth investigating further. However, the observed night-time regulation in autumn, winter and spring may be an artefact of T_e-model placement beneath rocks (Wills and Beaupre 2000). In particular, because of the limited number of

models placed beneath and on the edges of rocks (N = seven in autumn, six in winter, seven in spring), the actual T_es may not be a reliable estimate of available T_bs resulting in underestimates of thermal habitat quality, subsequently portraying an unrealistically high extent of thermoregulation.

Four exceptionally hot days were observed during the summer field-trial when the majority of T_es exceeded T_p both in the open (85.7%) and within crevices (68.4%) and reached values of up to 63.6°C. The temporal variation in T_e indicated that although lizards could maintain T_bs within T_p during the morning (7h00 – 11h00) by remaining within crevices, this feat was virtually impossible after midday (13h00 – 19h00). The thermal critical maxima (CT$_{max}$) of only three cordylids are currently known (*C. cordylus* 41.6 °C ± 1.0 °C; *C. niger* 41 °C ± 0.6 °C; *C. oelofseni* 40.8 °C ± 0.5 °C) of which the mean is 41.1 °C (Clusella-Trullas *et al.* 2009). The mean preferred temperatures of all three these cordylids exceed that of *C. cataphractus* by at least 2 °C (Clusella-Trullas *et al.* 2007; Chapter 2) and CT$_{max}$ may therefore also vary. The frequency distribution of T_bs indicates that nearly two percent of T_bs exceeded 39 °C and the highest measurement was 40.2 °C. The temporal and spatial distribution of T_es suggests that lizards reached such high temperatures involuntarily whilst being beneath rocks and in fact, not a single T_b recorded from 14h00 to 18h00 was below the upper bound of T_p. Body temperatures exceeding T_p are more harmful than those of equal magnitude below T_p (Huey 1982; Huey and Kingsolver 1993; Angilletta *et al.* 2006; Angilletta 2009), and T_bs exceeding CT$_{max}$ eventually results in death (Cowles and Bogert 1944). The high T_bs observed in *C. cataphractus* not only poses a risk to adults, but seeing that females are still gravid during summer (Flemming and Mouton 2002); foetuses may also be at risk.

Reptiles are known to exhibit behavioural and/or physiological plasticity to counteract the effects of extreme temperatures (Huey 1982). Firstly, extreme temperature can be buffered through behavioural thermoregulation (Huey *et al.* 2003; Huey and Tewksbury 2009). The high mean T_bs observed in *C. cataphractus* on hot summer days, and the fact that these mean T_bs were not lower than mean crevice T_e during the warmest time of day

however suggests that behavioural or physiological thermoregulation was insufficient to lower T_bs (to within T_p), resulting in temporary hyperthermia.

Secondly, certain reptiles may buffer the seasonal incidence of extreme temperatures by altering biological set points such as T_p and CT_{max} through physiological changes (reversible phenotypic plasticity) (Seebacher 2005). Neither CT_{max} nor the upper and lower lethal temperatures of *C. cataphractus* are currently known, but the determined T_p did not vary significantly among the warm autumn and cooler spring periods (Chapter 2). The CT_{max} of reptiles may however vary seasonally (Mueller 1969) and future studies should explore this possibility in *C. cataphractus*. It may well be that *C. cataphractus* either exhibits significant seasonal variation in CT_{max} or simply a high CT_{max}, therefore enabling them to remain unharmed within crevices during exceptionally warm periods.

Thirdly, certain reptiles may evade extreme temperatures through seasonal shifts in retreat site selection (Webb and Shine 1998; Kearney and Predavec 2000; Kearney 2002; Shah *et al.* 2004). For example, Kearney and Predavec (2000) found that the seasonal shifts in crevice preference in *Christinus marmoratus* are essential for survival during summer. Moreover, Webb and Shine (1998) found that the majority of *Hoplocephalus bungaroides* snakes moved from rock outcrops to cooler woodland habitats during the warmer summer. Visagie *et al.* (2002) investigated the intergroup movement patterns of *C. cataphractus* from March to November in six groups inhabiting relatively small rocks which (due to the high surface to volume ratio) are expected to become warm during the day and cool at night. Although numerous individuals exchanged groups, none of the rocks were evacuated at any given time suggesting the absence of whole-group migrations. Further exploration of thermal habitat quality among large and small rocks as well as seasonal movement patterns of lizards as a function of the thermal quality and size of rocks will be profitable in *C. cataphractus*.

Fourthly, reptiles may benefit from short term movements (shuttling) to thermally more favourable microsites during extreme temperatures (Grant and Dunham 1988). Although movement to cooler sites is expected in *C. cataphractus* during warm summer days, the

close correspondence between T_b and crevice-T_e indicates that they indeed did not move to larger boulders. The mean T_e in the open exceeded 50 $^{\circ}$C from 12h00 to 16h00 during the warmest experimental day, clearly trapping lizards within crevices, and any attempt to seek alternative refuges may be fatal under such conditions, especially for a sluggish slow-moving lizard such as *C. cataphractus*.

Extinction due to climate change is a real threat to lizards. Sinervo *et al.* (2010) surveyed 48 *Sceloporus* lizard species from 2006 to 2008 at 200 Mexican localities, previously sampled between 1975 and 1995, and found local extinction at 12 % of the sites. In a mathematical model (validated with current extinction records) Sinervo *et al.* (2010) predicted that 56 % of the viviparous and 46 % of the oviparous populations in Mexico will be extinct by 2060 if climate change continues unabated. Sinervo *et al.* (2010) suggested that extinction risk is significantly related to low T_b (typical in viviparous lizards) in Mexican *Sceloporus* lizards and that the extinction risk of viviparous lizards were double that of oviparous ones. The high T_bs observed during summer in combination with the fact that *C. cataphractus* is viviparous, carrying foetuses during the warmest part of the year (Flemming and Mouton 2002), and exhibits the lowest T_p recorded among cordylids to date (Chapter 2), suggest extinction risk (related to global climate change) to be high in the species (Sinervo *et al.* 2010).

3.6 Conclusion

The thermal habitat of *C. cataphractus* varied significantly as a function of the time of year as well as at micro-spatial scale around rocks, both as a function of distance from crevice edge and relative direction around rocks. *Cordylus cataphractus* males are known to be highly territorial when occurring in groups and the variation in T_e around rocks therefore provide an incentive for intra group competition for thermal habitat quality. The thermal habitat provided suitable T_es which *C. cataphractus* could access through behavioural thermoregulation during summer, autumn and spring. Typical winter days however provided virtually no favourable T_es and as expected the T_bs recorded at that time were equally low suggesting thermoconformity. The overall mean of field body temperatures observed during summer is the lowest recorded in the family to date corresponding to the lower preferred temperature range of *C. cataphractus*. *Cordylus cataphractus* performed active thermoregulation (expending time and/or energy (costs) to either lower or increase T_b to be within T_p) during summer, autumn and spring, and the accuracy of thermoregulation (i.e. absolute deviation of T_b from T_p) varied proportional to thermal quality suggesting uniform thermoregulatory investment among seasons. Preliminary data further suggest active thermoregulation (by seeking favourable T_es) at night which could either have taken place through microsite selection or huddling, or both. Annual surface activity patterns reported for *C. cataphractus* (Visagie 2001; Effenberger and Mouton 2007) correspond to micro-spatial distribution of favourable T_es during autumn and spring and may therefore be a direct function of the thermal habitat. It is however more likely that *C. cataphractus'* activity cycles are a function of temperature in combination with food availability and other factors such as predation risk, as has been suggested in other lizards (Diaz *et al.* 2005; Sears 2005). Although *C. cataphractus* has been reported to exhibit repressed surface activity during late summer, the current results suggest that lizards indeed emerged from crevices at the time. Four exceptionally warm days were observed during the summer field trial during which individuals were clearly forced to remain within crevices for the majority of the day. Overheating was a real risk even within crevices, especially for groups occurring beneath

small rocks. Although shifts to cooler larger rocks during such conditions would have benefited the animals, the current data indicate that they did not, and reached T_bs of up to 40.2^{o}C. These temperatures were recorded shortly prior to parturition and foetuses may therefore also be at risk.

3.7 Appendix

Table A1. Mean operative environmental temperatures (T_e), thermal habitat quality (d_e), field body temperatures (T_b), accuracy of thermoregulation (d_b), effectiveness of thermoregulation ($d_e - d_b$) and thermal exploitation (E_x) of a coastal population of *C. cataphractus* recorded and/or calculated during summer, autumn, winter and spring. Values represent means ± SD calculated from measurements taken at 15 minute intervals (7h00 to 19h00) across sample days during the respective seasons.

Season	T_e-model Placement	T_e (°C)	d_e (°C)	T_b (°C)	d_b (°C)	$d_e - d_b$	E_x (%) (10h00-19h00)
Summer	Crevice	25.4 ± 4.0	2.7 ± 2.8				
	Crevice & Open	28.3 ± 7.0	3.5 ± 3.7	25.8 ± 3.7	3.7 ± 2.7	2.0 ± 2.4	53.2 ± 35.5
	Open	32.5 ± 8.1	4.6 ± 4.4				
Summer*	Crevice	34.3 ± 4.7	3.1 ± 3.0				
	Crevice & Open	37.5 ± 7.8	6.1 ± 6.5	33.4 ± 4.6	2.8 ± 2.2	3.37 ± 2.9	21.7 ± 8.4
	Open	42.3 ± 8.8	10.5 ± 7.5				
Autumn	Crevice	26.2 ± 4.9	2.2 ± 2.8				
	Crevice & Open	29.5 ± 7.5	3.3 ± 3.8	27.0 ± 4.2	1.6 ± 2.2	1.8 ± 2.3	58.5 ± 33.8
	Open	31.2 ± 8.0	3.8 ± 4.1				
Winter	Crevice	14.4 ± 3.5	12.5 ± 3.5				
	Crevice & Open	16.3 ± 5.4	10.6 ± 5.1	16.0 ± 3.4	10.9 ± 3.3	0.5 ± 4.2	2.6 ± 4.2
	Open	16.8 ± 5.8	10.1 ± 5.4				
Winter*	Crevice	17.6 ± 5.4	9.3 ± 5.2				
	Crevice & Open	20.0 ± 7.3	7.6 ± 6.3	20.4 ± 7.1	7.2 ± 6.0	3.5 ± 4.7	18.4 ± 22.2
	Open	20.7 ± 7.6	7.0 ± 6.5				(11h00 - 18h00)
Spring	Crevice	19.5 ± 6.0	8.4 ± 5.3				
	Crevice & Open	24.3 ± 9.0	6.6 ± 5.6	24.9 ± 8.2	5.1 ± 5.9	1.5 ± 3.9	39.7 ± 18.6
	Open	25.9 ± 9.3	6.0 ± 5.5				

*Recorded during exceptionally warm days (*N* (days) = four summer, two winter)

Table A2. Hourly means (± 1SD) of operative environmental temperatures (T_e) and thermal habitat quality (d_e) in a coastal population of *C. cataphractus* during summer, autumn, winter and spring. Thermal habitat quality expresses the degree of deviation of operative environmental temperatures (T_e) from the preferred temperature range (T_p). A d_e of zero indicates perfect thermal habitat quality (i.e. $T_e = T_p$) suggesting the potential of passive thermoconformation (Hertz *et al.* 1993). Values represent hourly means of values calculated from T_e measurements taken at 15 minute intervals across sample days.

Time	d_e (°C)			
	Summer	Autumn	Winter	Spring
8h00	6.6 ± 2.7	7.0 ± 3.7	16.7 ± 2.3	14.8 ± 5.2
9h00	5.1 ± 2.8	4.3 ± 3.3	15.8 ± 1.9	10.0 ± 6.3
10h00	4.1 ± 2.8	3.2 ± 2.8	14.0 ± 2.3	6.3 ± 6.7
11h00	4.4 ± 3.4	3.4 ± 3.3	11.2 ± 3.9	5.0 ± 5.7
12h00	4.5 ± 4.3	4.0 ± 4.1	8.9 ± 4.8	5.2 ± 4.5
13h00	4.3 ± 4.7	3.8 ± 4.5	7.5 ± 4.7	5.4 ± 4.0
14h00	3.8 ± 4.5	4.2 ± 4.9	6.2 ± 4.7	4.4 ± 3.7
15h00	2.9 ± 3.7	3.8 ± 4.5	5.6 ± 4.5	3.8 ± 3.6
16h00	2.1 ± 2.9	2.4 ± 3.1	6.5 ± 4.0	3.8 ± 3.3
17h00	1.2 ± 2.0	1.2 ± 2.1	9.0 ± 2.9	4.7 ± 3.4
18h00	0.8 ± 1.3	0.6 ± 1.1	12.1 ± 2.0	6.4 ± 3.9
19h00	1.6 ± 1.6	1.7 ± 1.6	14.0 ± 1.5	9.1 ± 3.4

Table A3. Hourly means (± 1SD) of operative environmental temperatures (T_e) and thermal habitat quality (d_e) in a coastal population of *C. cataphractus* during summer, autumn, winter and spring. Values represent hourly means of T_e measurements recorded with copper lizard models at 15 minute intervals across sample days.

Time	T_e (^{o}C)					
	Summer	Summer*	Autumn	Winter	Winter*	Spring
8h00	20.4 ± 3.1	27.9 ± 4.1	19.4 ± 4.1	10.1 ± 2.3	9.5 ± 3.0	12.7 ± 5.2
9h00	22.8 ± 4.7	31.2 ± 5.6	23.3 ± 5.1	11.0 ± 1.9	12.0 ± 4.6	17.7 ± 6.7
10h00	26.4 ± 6.6	34.7 ± 6.6	26.8 ± 6.3	12.8 ± 2.3	15.1 ± 4.9	22.2 ± 7.7
11h00	28.9 ± 7.8	37.5 ± 7.4	30.2 ± 7.4	15.6 ± 4.0	19.4 ± 5.3	26.4 ± 8.7
12h00	30.8 ± 8.3	40.0 ± 8.4	32.4 ± 7.8	18.1 ± 5.3	23.1 ± 5.9	29.0 ± 8.9
13h00	31.7 ± 8.2	41.5 ± 8.4	33.7 ± 7.4	19.8 ± 5.6	26.0 ± 6.0	30.7 ± 8.9
14h00	32.0 ± 7.5	42.3 ± 8.2	34.5 ± 7.4	21.2 ± 5.5	27.1 ± 5.7	30.4 ± 7.8
15h00	31.8 ± 6.4	42.4 ± 7.5	34.6 ± 6.7	21.5 ± 4.9	26.5 ± 4.7	29.2 ± 7.2
16h00	31.1 ± 5.3	40.6 ± 6.1	33.4 ± 5.1	20.3 ± 4.1	25.1 ± 4.2	28.0 ± 6.8
17h00	29.7 ± 4.2	39.4 ± 5.2	31.5 ± 4.2	17.8 ± 2.9	22.3 ± 3.8	25.4 ± 6.5
18h00	28.1 ± 3.0	37.2 ± 3.9	28.8 ± 3.4	14.6 ± 2.0	18.7 ± 3.0	21.0 ± 5.4
19h00	25.8 ± 2.2	35.6 ± 2.6	25.4 ± 2.8	12.8 ± 1.5	15.4 ± 2.2	18.6 ± 4.0

*Recorded during exceptionally warm days (N (days) = four summer, two winter)

Table A4. Hourly means (± 1SD) of operative environmental temperatures (T_e) recorded on the edges of and within crevices in a coastal population of *C. cataphractus* during summer, autumn, winter and spring. Values represent hourly means of T_e measurements recorded with copper lizard models at 15 minute intervals across sample days.

Time	Crevice T_e (^{o}C)					
	Summer	Summer*	Autumn	Winter	Winter*	Spring
8h00	20.2 ± 2.5	27.8 ± 3.6	20.1 ± 3.6	10.5 ± 2.0	10.3 ± 3.1	12.7 ± 4.5
9h00	21.3 ± 3.3	29.3 ± 4.4	21.4 ± 3.3	10.9 ± 1.7	11.5 ± 3.6	14.6 ± 5.2
10h00	23.0 ± 4.1	31.4 ± 4.6	22.9 ± 3.4	11.7 ± 1.5	13.5 ± 3.9	16.4 ± 5.9
11h00	24.5 ± 4.3	33.2 ± 4.5	24.7 ± 3.7	12.8 ± 1.8	15.3 ± 4.1	18.1 ± 5.9
12h00	25.8 ± 4.1	34.8 ± 4.3	26.3 ± 4.3	14.0 ± 2.1	17.3 ± 4.2	19.7 ± 5.0
13h00	26.6 ± 3.7	36.0 ± 3.9	27.4 ± 4.3	15.0 ± 2.5	19.7 ± 4.0	21.4 ± 5.0
14h00	27.1 ± 3.3	36.6 ± 3.4	28.1 ± 4.2	16.0 ± 2.7	21.5 ± 3.4	21.9 ± 4.0
15h00	27.6 ± 2.9	37.2 ± 3.0	28.8 ± 4.1	17.0 ± 3.2	22.5 ± 2.8	22.1 ± 3.8
16h00	27.8 ± 2.5	36.8 ± 3.0	29.2 ± 3.8	18.0 ± 4.0	23.2 ± 3.6	23.1 ± 5.2
17h00	27.4 ± 2.2	36.5 ± 3.0	29.5 ± 4.3	17.3 ± 3.7	22.8 ± 4.6	23.0 ± 6.1
18h00	26.9 ± 2.0	35.8 ± 2.7	28.7 ± 3.9	15.3 ± 2.6	19.8 ± 3.5	21.6 ± 5.7
19h00	26.1 ± 2.0	35.8 ± 2.3	26.7 ± 2.8	13.7 ± 1.6	16.5 ± 2.2	19.3 ± 4.2

*Recorded during exceptionally warm days (N (days) = four summer, two winter)

Table A5. Hourly means (± 1SD) of field body temperatures (T_b) recorded in a coastal population of *C. cataphractus* during summer, autumn, winter and spring. Values represent hourly means of T_b measurements taken at 15 minute intervals across sample days.

Time	T_b (°C)					
	Summer	Summer*	Autumn	Winter	Winter*	Spring
8h00	19.6 ± 0.9	25.9 ± 2.8	21.6 ± 2.0	12.6 ± 1.4	11.6 ± 1.5	13.1 ± 4.2
9h00	20.5 ± 0.9	26.8 ± 2.6	22.0 ± 2.2	12.4 ± 1.4	11.9 ± 1.9	14.7 ± 6.7
10h00	21.9 ± 1.2	28.7 ± 3.0	22.5 ± 2.5	12.6 ± 1.2	13.0 ± 2.6	17.2 ± 7.4
11h00	23.7 ± 1.4	30.9 ± 3.0	24.0 ± 2.9	13.2 ± 1.1	14.9 ± 3.6	26.4 ± 8.3
12h00	25.5 ± 1.4	33.1 ± 2.5	26.1 ± 3.2	14.1 ± 1.0	18.2 ± 6.1	29.5 ± 6.9
13h00	27.1 ± 1.4	35.0 ± 2.1	27.9 ± 3.0	15.3 ± 1.5	21.9 ± 7.6	32.0 ± 2.5
14h00	28.4 ± 1.6	36.1 ± 1.8	28.9 ± 2.8	17.3 ± 3.5	25.4 ± 5.1	32.1 ± 3.1
15h00	29.2 ± 1.8	37.1 ± 1.6	29.5 ± 2.6	18.9 ± 3.4	27.2 ± 3.4	29.8 ± 3.3
16h00	29.4 ± 1.9	37.3 ± 1.3	30.2 ± 2.4	19.7 ± 2.9	27.1 ± 3.6	28.2 ± 3.9
17h00	29.1 ± 1.8	37.1 ± 1.2	30.5 ± 2.2	19.3 ± 1.8	27.3 ± 3.9	27.2 ± 4.0
18h00	28.4 ± 1.8	36.6 ± 1.2	30.4 ± 2.1	18.6 ± 1.3	24.6 ± 2.2	25.9 ± 4.3
19h00	27.4 ± 1.8	36.5 ± 1.0	29.8 ± 2.1	17.6 ± 0.9	21.7 ± 0.8	23.3 ± 3.1

*Recorded during exceptionally warm days (*N* (days) = four summer, two winter)

Table A6. Hourly means (± 1SD) of thermoregulatory accuracy (d_b) in a coastal population of *C. cataphractus* during summer, autumn, winter and spring. The accuracy of thermoregulation (d_b) expresses the degree of deviation between field body temperature (T_b) and the preferred temperature range (T_p). A d_b value of zero indicates perfect accuracy (i.e. $T_b = T_p$) (Hertz *et al.* 1993). Values represent hourly means of values calculated from T_b measurements taken at 15 minute intervals across sample days.

Time	d_b (°C)			
	Summer	Autumn	Winter	Spring
8h00	7.2 ± 0.9	4.7 ± 2.0	14.2 ± 1.4	14.4 ± 4.2
9h00	6.3 ± 0.9	4.4 ± 1.9	14.4 ± 1.4	13.3 ± 5.5
10h00	4.9 ± 1.2	4.0 ± 2.0	14.2 ± 1.2	11.2 ± 5.8
11h00	3.1 ± 1.4	2.8 ± 1.9	13.6 ± 1.1	4.8 ± 5.4
12h00	1.4 ± 1.2	1.4 ± 1.5	12.7 ± 1.0	3.3 ± 3.9
13h00	0.4 ± 0.7	0.6 ± 1.0	11.5 ± 1.5	1.3 ± 1.7
14h00	0.1 ± 0.5	0.3 ± 0.8	9.6 ± 2.9	1.2 ± 1.4
15h00	0.1 ± 0.4	0.3 ± 0.8	8.0 ± 3.0	0.9 ± 1.5
16h00	0.1 ± 0.4	0.2 ± 0.8	7.2 ± 2.7	1.5 ± 1.9
17h00	0.1 ± 0.3	0.2 ± 0.7	7.5 ± 1.8	2.1 ± 2.1
18h00	0.2 ± 0.4	0.2 ± 0.6	8.2 ± 1.3	3.0 ± 2.8
19h00	0.5 ± 0.8	0.1 ± 0.5	9.2 ± 0.9	4.3 ± 2.8

Table A7. Hourly means (± 1SD) of thermoregulatory effectiveness ($d_e - d_b$) in a coastal population of *C. cataphractus* during summer, autumn, winter and spring. The effectiveness of thermoregulation ($d_e - d_b$) expresses the degree of departure from thermoconformity ($d_e - d_b$ = 0: perfect thermo conformity). Negative $d_e - d_b$s generally indicate the avoidance of thermally suitable microsites (Blouin-Demers and Weatherhead 2001). Values represent hourly means of values calculated from T_e and T_b measurements taken at 15 minute intervals across sample days.

Time	$d_e - d_b$ (°C)			
	Summer	Autumn	Winter	Spring
8h00	-0.6 ± 1.2	2.4 ± 1.7	3.5 ± 2.4	0.4 ± 1.9
9h00	-1.2 ± 1.2	-0.1 ± 1.8	2.2 ± 2.1	-3.3 ± 3.0
10h00	-0.7 ± 1.2	-0.6 ± 1.8	0.6 ± 2.0	-4.9 ± 4.2
11h00	1.3 ± 1.4	1.0 ± 2.3	-1.8 ± 2.5	0.3 ± 5.1
12h00	3.1 ± 1.3	2.9 ± 2.2	-3.3 ± 3.3	1.2 ± 3.5
13h00	3.9 ± 1.1	3.4 ± 2.2	-3.4 ± 3.6	4.1 ± 2.1
14h00	3.7 ± 0.6	3.9 ± 2.1	-2.7 ± 4.1	3.2 ± 1.9
15h00	2.8 ± 0.7	3.6 ± 1.9	-1.5 ± 4.1	3.0 ± 1.7
16h00	1.9 ± 0.7	2.1 ± 1.3	0.2 ± 3.4	2.3 ± 1.9
17h00	1.1 ± 0.7	1.0 ± 0.9	2.3 ± 2.6	2.6 ± 1.8
18h00	0.6 ± 0.6	0.4 ± 0.6	4.5 ± 2.0	3.5 ± 1.8
19h00	1.1 ± 0.9	1.6 ± 1.4	5.6 ± 1.4	4.8 ± 1.0

Table A8. Hourly means (± 1SD) of thermal exploitation (E_x) in a coastal population of *C. cataphractus* during summer, autumn, winter and spring. Thermal exploitation describes the degree to which a reptile exploits the thermally favourable opportunities for precise thermoregulation, particularly describing the time-fraction (%) during which T_b equals T_p when permissive in a particular habitat (Christian and Weavers 1996). Values represent hourly means of values calculated from T_e and T_b measurements taken at 15 minute intervals across sample days.

Time	E_x (%)			
	Summer	Autumn	Winter	Spring
8h00	0	0	-	0
9h00	0	2.0 ± 3.5	-	33.3 ± 28.9
10h00	0	4.8 ± 4.5	-	5.3 ± 5.3
11h00	1.1 ± 2.8	16.3 ± 7.8	0	21.7 ± 20.2
12h00	13.3 ± 10.0	31.7 ± 14.5	0	37.5 ± 10.8
13h00	51.1 ± 21.9	55.6 ± 16.7	0	52.1 ± 7.2
14h00	80.8 ± 13.5	70.2 ± 24.3	4.6 ± 8.0	44.4 ± 5.6
15h00	87.9 ± 10.5	82.4 ± 14.6	7.3 ± 7.9	56.7 ± 12.6
16h00	85.2 ± 17.7	93.5 ± 5.1	6.4 ± 8.0	48.3 ± 12.6
17h00	81.1 ± 17.6	87.3 ± 7.7	0	35.2 ± 3.2
18h00	73.1 ± 22.4	84.5 ± 6.8	-	56.4 ± 4.4
19h00	58.3 ± 30.2	86.1 ± 5.1	-	55.6 ± 38.5

Table A9: Generalized linear mixed model analyses (PROC GLIMMIX) describing the effect of T_e-model placement relative to crevices on the (a) operative environmental temperatures (T_e) and (b) thermal habitat quality (d_e), of a coastal population of *C. cataphractus* during summer, autumn, winter and spring.

a) T_e

Source of Variance	Summer			Autumn			Winter			Spring		
	df	F	P	df	F	P	df	F	P	df	F	P
Day	10,420	127.58	< 0.01	8,144	112.28	< 0.01	9,216	44.96	< 0.01	4,104	73.48	< 0.01
Hour	11,396	1059.17	< 0.01	11,132	337.85	< 0.01	11,198	464.14	< 0.01	11,220	184.04	< 0.01
Distance	6,36	15.79	< 0.01	6,12	3.32	0.04	6,18	1.87	0.14	6,20	4.35	0.01
Hour*Distance	66,396	78.46	< 0.01	66,132	14.19	< 0.01	66,198	12.44	< 0.01	66,220	6.99	< 0.01

b) d_e

Source of Variance	Summer			Autumn			Winter			Spring		
	df	F	P	df	F	P	df	F	P	df	F	P
Day	10,420	20.99	< 0.01	8,144	15.34	< 0.01	9,216	45.63	< 0.01	4,104	41.07	< 0.01
Hour	11,396	212.17	< 0.01	11,132	59.41	< 0.01	11,198	539.7	< 0.01	11,220	98.2	< 0.01
Distance	6,36	4.82	< 0.01	6,12	2.14	0.12	6,18	2.1	0.10	6,20	2.65	0.05
Hour*Distance	66,396	51.71	< 0.01	66,132	5.33	< 0.01	66,198	13.69	< 0.01	66,220	3.71	< 0.01

Table A10: Generalized linear mixed model analyses (PROC GLIMMIX) describing the effect of T_e-model placement (around rocks) relative to the four major wind directions on the (a) operative environmental temperatures (T_e) and (b) thermal habitat quality (d_e) of a coastal population of *C. cataphractus* during summer, autumn, winter and spring. Analyses were performed on hourly means of T_e and d_e.

a) T_e

Source of Variance	Summer			Autumn			Winter			Spring		
	df	F	P	df	F	P	df	F	P	df	F	P
Day	10,200	47.5	< 0.01	8,112	111.97	< 0.01	9,189	46.37	< 0.01	4,88	66.35	< 0.01
Hour	11,187	594.81	< 0.01	11,121	384.15	< 0.01	11,198	512.33	< 0.01	11,209	224.74	< 0.01
Direction	3,17	3.97	0.03	3,11	5.18	0.02	3,18	10.22	< 0.01	3,19	4.42	0.02
Hour*Direction	33,187	35.55	< 0.01	33,121	22.04	< 0.01	33,198	19.79	< 0.01	33,209	17.77	< 0.01

b) d_e

Source of Variance	Summer			Autumn			Winter			Spring		
	df	F	P	df	F	P	df	F	P	df	F	P
Day	10,200	13.17	< 0.01	8,112	17.56	< 0.01	9,189	44.64	< 0.00	4,88	26.05	< 0.01
Hour	11,187	125.25	< 0.01	11,121	63.51	< 0.01	11,198	569.13	< 0.00	11,209	117.9	< 0.01
Direction	3,17	6.63	< 0.01	3,11	5.08	0.02	3,18	9.33	< 0.00	3,19	16.52	< 0.01
Hour*Direction	33,187	36.09	< 0.01	33,121	16.95	< 0.01	33,198	18.21	< 0.00	33,209	15.4	< 0.01

Table A11: Generalized linear mixed model analyses (PROC GLIMMIX) describing the effect of time and gender on the field body temperatures (T_b), accuracy of thermoregulation (d_b) and effectiveness of thermoregulation ($d_e - d_b$) of a coastal population of *C. cataphractus* across summer, autumn, winter and spring.

Effect	df	T_b		d_b		$d_e - d_b$	
		F	P	F	P	F	P
Hour	11,198	366.16	< 0.01	362.49	< 0.01	36.99	< 0.01
Day	10,145	23.41	< 0.01	10.05	< 0.01	3.82	< 0.01
Season	3,11	64.99	< 0.01	234.96	< 0.01	3.82	0.04
Gender	1,11	0.58	0.46	0.87	0.38	0.5	0.49
Season*Gender	3,11	0.42	0.74	0.52	0.68	0.48	0.70

Chapter 4

Geographical patterns, with reference to seasonality in thermoregulation in the group-living lizard, *Cordylus cataphractus*

4.1 Abstract

The cost-benefit model of thermoregulation predicts thermoregulatory investment in proportion to thermoregulatory costs. The model has been experimentally validated and is widely accepted. Recent investigations on cold-temperate reptiles have however brought into question the model's validity to all reptiles. Permanent group-living is uncommon among squamates. In an arid environment, the permanent group-living phenomenon is expected to amplify energetic constraints on site specific insectivorous species, affecting behavioural processes such as thermoregulation. The aim of the current study was twofold. The first objective was to compare the thermal habitat and subsequent thermoregulatory patterns of the permanent group-living *Cordylus cataphractus* in a coastal (western range limit) and inland population (eastern range limit) during the respective annual peaks in food scarcity (dry autumn) and food abundance (wet spring). Previous studies have reported low surface activity in hot, dry periods when food is scarce. The second objective was to establish whether the thermoregulatory activity *C. cataphractus* varies among seasons in response to relative thermal habitat quality (as predicted by the cost-benefit model of thermoregulation), or whether the negative effect of living in groups related to increased food constraints, dictates thermoregulatory activity. Thermoregulatory assessments were based on several indices namely: thermal habitat quality (d_e), accuracy of thermoregulation (d_b), the effectiveness of thermoregulation ($d_e - d_b$) and thermal exploitation (E_x). These indices were collectively calculated from: the preferred temperature range (T_p) of *C. cataphractus* (determined in a laboratory thermal gradients), operative environmental temperatures (T_e) (measured using copper lizard models in the field), and field body temperatures (T_b) (recorded with modified iButton temperature loggers). The current results indicate that

copper T_e-models used for *C. cataphractus* provide realistic equilibrium (body) temperatures when validated properly, and that the use of energy absorbance measurements through a wider electromagnetic spectrum (well into the IR spectrum) results in more accurate T_e-models. The effectiveness and success of thermoregulation did not vary significantly among populations during autumn. Conversely, in spring (annual activity peak of *C. cataphractus*); lizards in the coastal population (generally larger groups) thermoregulated more successfully than lizards in the inland population (generally smaller groups). The higher thermoregulatory success in the coastal population was likely due to reduced predation risk associated with increased group-size, in particular, due to relaxed time budgets and by allowing individuals to move further from crevices. Group-size and hence the group-living life strategy may therefore confer advantages in terms of thermoregulatory capacity in *C. cataphractus*. Lizards from both populations thermoregulated more accurately in autumn than spring, and as a function of relative thermal habitat quality, rather than food availability, therefore supporting the cost-benefit model of thermoregulation in *C. cataphractus*, and indicating that the group-living life strategy (in relation to amplified food scarcity) does not reduce thermoregulatory capacity.

Key words: Group-living, lizard, thermoregulation, cost-benefit model, food constraints, geographic variation.

4.2 Introduction

Thermoregulation is an active (energy consuming) process employed by most reptiles to maintain body temperatures near to or within their target preferred temperature range (T_p) (Licht *et al.* 1966). Since reptiles generally rely less on metabolic heat production, body temperature (T_b) is largely a function of ambient temperatures (T_as) and availability of radiation energy (Pough 1980; Huey 1982; Angilletta 2009). Bakken and Gates (1975) suggested the use of an operative environmental temperature (T_e), integrating environmental temperatures (T_a) (including conductivity properties), convection effects and available radiation in a steady-state temperature (i.e. T_e) of an organism in a particular microclimate in the absence of metabolic heat production and evaporative cooling. When experiencing extreme temperatures (i.e. T_e far from T_p, high or low) thermoregulation is needed to maintain T_bs within the T_p range, or reduce variation in body temperatures (Angilletta 2009), otherwise performance may be compromised (Stevenson *et al.* 1985; Blouin-Demers and Weatherhead 2001). An array of behavioural and physiological mechanisms that facilitate thermoregulation have been identified which include: selective inactivity, postural adjustments, shuttling, microsite selection, orientation, vasoconstriction, vasodilatation and panting (Bartholomew 1982; Stevenson 1985; Bauwens *et al.* 1996; Angilletta 2009). Because behavioural thermoregulation infers time and/or energy costs (but also mortality and missed opportunity costs), the use of behavioural means to avoid or select environmental temperatures may vary among species (Ruibal 1961). Two strategies for T_b management (when using a cost-benefit approach) have been identified in ectotherms: on the one extreme of the continuum, thermoconformation, and on the other, thermoregulation (Ruibal 1961; Hertz *et al.* 1993; Blouin-Demers and Nadeau 2005). The effectiveness of thermoregulation (along the conformity-regulation continuum) may vary at short and long term temporal and/or spatial scales within a species, where individuals may shift from being strict to moderate thermoregulators, or even undergo a total strategy change, becoming thermoconformers (Huey 1974; Hertz *et al.* 1993; Schauble and Grigg 1998; Herczeg *et al.* 2008).

Active thermoregulation equates to increased costs related to energy and time, since time spent thermoregulating include basking, orientating and moving/shuttling that can be mutually exclusive with activities such as foraging or mating (Huey 1974; Grant and Dunham 1988; Blouin-Demers and Nadeau 2005) or other social activities in group-living species. In fact, seasonal variation in the effectiveness and success of thermoregulation in reptiles are, in most cases, associated with changes in thermal habitat quality (the deviation of available environmental temperatures from the range of preferred temperatures) (Hertz *et al.* 1993; Angilletta 2001), or other known thermoregulatory costs such as social behaviour (i.e. aggression or mating and courtship) (Schauble and Grigg 1998) and predation risk (Herczeg *et al.* 2008).

The cost-benefit model for ectotherm thermoregulation is a conceptual framework to explain/understand the selection of thermoregulation strategies along the conformity-regulation continuum with the associated cost–to–benefit ratios (Huey and Slatkin 1976). Based on warm temperate climates, Huey and Slatkin (1976) described the cost-benefit model of thermoregulation which suggests that ectotherms become thermoconformers (therefore not controlling T_b, being either hypo- or hyperthermic, but mostly hypothermic, limiting activity) when costs outweigh the benefits of maintaining a T_b within the preferred temperature range (T_p). The cost-benefit model has been validated experimentally (Withers and Campbell 1985; Herczeg *et al.* 2006; Herczeg *et al.* 2008) and is generally accepted by researchers (e.g. Hertz *et al.* 1993; Gvozdik 2002; Herczeg *et al.* 2006; Herczeg *et al.* 2008). The application of the Huey and Slatkin (1976) model in environments with extreme temperatures was however recently questioned in cold environments (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Weatherhead 2002; Blouin-Demers and Nadeau 2005). In extreme environments, cold or hot, the Huey and Slatkin (1976) model predict thermoconformity, but in these environments, the lack of thermoregulation would result in T_bs unfavourable for performance (Blouin-Demers and Weatherhead 2001). As an alternative, recent studies have shown that reptiles from extreme cold-temperate environments follow a different model, investing in thermoregulation even though the costs outweigh the benefits,

because the benefits of behavioural thermoregulation still outweigh the disadvantages of thermoconformity (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Weatherhead 2002; Row and Blouin-Demers 2006; Edwards and Blouin-Demers 2007).

The thermoregulation strategy selected for could be affected by general energetic constraints such as prolonged food scarcity (resulting in strict energy budgets). In these cases the drive to thermoregulate, even though performance (physiological functioning) may be compromised, may be abandoned because of energy budget constraints. For example, Lee (1980) found that poorly nourished *Anolis sagrei* thermoregulated less precisely than well-fed conspecifics providing support for the notion that food constraints and its effect on the animal may affect thermoregulation.

Cordylus cataphractus is a saxicolous sit-and-wait forager occurring in social groups of up to 58 individuals along the semi-arid to arid far-western parts of South Africa (Mouton *et al.* 1999; Mouton *et al.* 2000b; Effenberger and Mouton 2007). Group-living amplifies food constraints in harsh environments (Mouton *et al.* 2000a; Hayward 2008) and may therefore indirectly affect thermoregulation (Lee 1980). Group-living in isolated rock habitats in extreme environments may place further constraints on thermoregulation since density and social conflicts may affect microhabitat availability/selection to group members (Huey 1982; Chapter 3). It has been shown that *C. cataphractus* populations undergo seasonal food-stress (reduced food availability) that may affect outside crevice activity (Mouton *et al.* 2000a; Visagie 2001). The rationale being that without the possibility of obtaining food, no real benefit exists to be active on the surface of the rocks (Pyke *et al.* 1977), since activity will result in costs of thermoregulation or increased T_bs and associated metabolic energy expenditure as well as predation risk. Although the cost-benefit approach described by Huey and Slatkin (1976) is based on costs associated with thermoregulation, food stress and reduced surface activity could have indirect consequences for costs of thermoregulation. Whether the change in activity in a hot dry environment serve as a major constrain on thermoregulation, particularly to utilize the benefit of functioning within the preferred temperature range (T_p), is not known. Moreover, the limited energy budget may preclude

lizards being in the T_p range with increased metabolic energy costs associated. However, increased metabolic expenditure due to high T_bs is tentative since; Mouton *et al.* (2000b) have shown that *C. cataphractus* exhibits an exceptionally low resting metabolic rate at different T_as, 68.8 % lower than that known for any other cordylid.

The major expected cost incurred by group-living on *C. cataphractus* is suggested to be seasonally reduced food availability (Mouton *et al.* 2000a; Flemming and Mouton 2002; Hayward 2008). Although a cost to the animal, it is not a direct cost of thermoregulation and, in principle, not part of the Huey and Slatkin (1976) cost-benefit equation. In relation to *C. cataphractus*, the food cost of group-living is therefore not a cost of thermoregulation, yet it may affect/override the drive to thermoregulate, in particular by investing less in thermoregulation during the annual dry season, simply because of strict energy budgets.

Although the field of reptile thermal ecology is well established in the literature, only a limited number of studies exist in the African-context, of which none to date has explored population level variation in thermoregulation, or explored the cost-benefit model of thermoregulation. Although *C. cataphractus* is a relatively well-studied organism (e.g. Mouton *et al.* 1999; Mouton *et al.* 2000a; Mouton *et al.* 2000b; Visagie *et al.* 2002; Curtin *et al.* 2005; Costandius *et al.* 2006; Effenberger and Mouton 2007; Shuttleworth *et al.* 2008), little is known regarding its thermal ecology, especially with reference to the group-living phenomenon and the seasonal decrease in surface activity because of food stress and predator risk.

The primary objective of the current study was to characterize the thermal environments and subsequent patterns of thermoregulation in a coastal population of *C. cataphractus* (western range limit, generally with larger groups) and an inland population (eastern range limit, generally with smaller groups) during the respective annual peaks in expected food scarcity and availability (i.e. autumn and spring (Mouton *et al.* 2000a)). The assessment was performed by applying a suite of quantitative indices namely thermal habitat quality (d_e), thermoregulatory accuracy (d_b), effectiveness of thermoregulation ($d_e - d_b$), and thermal exploitation (E_x).

Specific questions addressed:

1. Does the thermal habitat quality of *C. cataphractus* and effectiveness and success of thermoregulation vary among an inland and coastal population during the dry autumn and more mesic spring as predicted by climatic data?

2. Does the success and effectiveness of thermoregulation by *C. cataphractus* vary seasonally in response to the relative thermal quality as predicted by the cost-benefit model of thermoregulation, or is thermoregulation dictated by the amplified energy constraints related to group-living?

4.3 Materials and Methods

4.3.1 Study area and animals

Data collection occurred during the autumn (April) and spring (September) of 2008. The coastal population inhabits a series of sandstone ridges near Elands Bay (Western Cape, South African ($32^{o}19'38.61"$S; $18^{o}21'35.78"$E)), which falls within the Langebaan Dune Strandveld vegetation region, with an annual precipitation of 200 mm (South African Weather Service; Mucina and Rutherford 2006) (Figure 4.1). Fog (originating from the cold Benguela Atlantic Current) and dew contribute to overall moisture (Mucina and Rutherford 2006; Janse van Rensburg 2009). Fog incidence peaks during the warm dry months of March, April and May and is least in September (Olivier 2002). The inland population is located in the Matjiesrivier Nature Reserve (Western Cape, South Africa, ($32^{o}29'01.53"$S; $19^{o}21'31.18"$E)), ~120km south-east of the coastal population. The locality has an annual precipitation of 210 mm (South African Weather Services; Mucina and Rutherford 2006) (Figure 4.1). The area is scattered with quartzite sandstone boulders that provide the ideal habitat for *C. cataphractus*, yet, population density is low, with a maximum-recorded group-size of six (Retief 2000). In contrast, the coastal study area is densely populated by *C. cataphractus* with group-sizes varying between two and 25 individuals (Visagie 2001). Mean monthly maximum ambient temperatures (T_a) are lower at the inland than coastal population for the majority of the year, but, corresponds closely among populations during the warm summer period, whereas mean min T_a is consistently lower at the inland population throughout the year (Figure 4.1). Solar radiation corresponds among populations during the cooler months yet is higher at the inland population during the warmer months (Figure 4.1). The fact that solar radiation follows an opposite trend (among populations) than T_a-max as well as the consistent difference in T_a-min among populations suggests that the corresponding T_a-max during the warm period is due to higher solar radiation at the inland population. Monthly estimates of rainfall correspond relatively among localities during autumn, yet, being higher at the coastal population during spring.
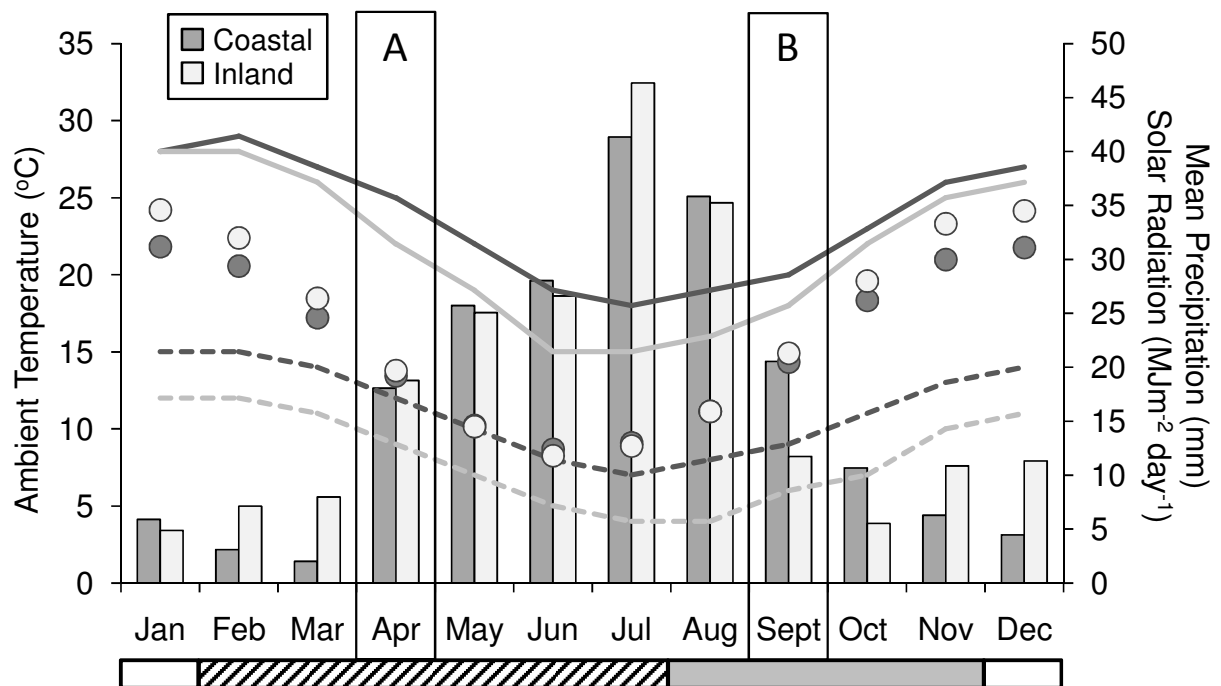
Figure 4.1. Mean monthly rainfall (vertical bars), minimum and maximum ambient temperatures (lines) and solar radiation (circles) for the coastal (dark grey) and inland (light grey) localities (rainfall: 1998-2008, SA Weather Services; temperatures and solar radiation: A van Niekerk, unpublished data). Vertical bars indicate the respective sampling periods (A: autumn; B: spring). The horizontal bar indicates seasonal activity in *C. cataphractus* as described in the literature (Visagie 2001; Effenberger and Mouton 2007) (slanted-line: repressed activity; grey: normal activity; clear: activity unknown).

4.3.2 Environmental operative temperature (T_e)

4.3.2.1 T_e-model construction

Operative environmental temperatures (T_e) represent a null model for thermoregulation (i.e. T_b in the absence of thermoregulation), used to map specific thermal habitats (Hertz *et al.* 1993). Operative environmental temperatures (T_e) were measured with hollow copper models, constructed through electroplating according to the protocol described by Bakken and Gates (1975) (Figure 4.2). In brief, lizard casts were manufactured from Wood's Alloy (melting point 70°C) in a latex mould constructed from a single deceased fixated lizard. The alloy provided an electric conductible surface to which a copper layer (~0.5mm) was then electroplated. The plated casts were heated in an oven at approximately 80°C, allowing the alloy to seep out through two manually made holes. To accurately represent heat absorption of live lizards, models were painted in correspondence to lizard skin colouration and T_e therefore represents the maximum attainable body temperature in a particular microhabitat at a particular time.
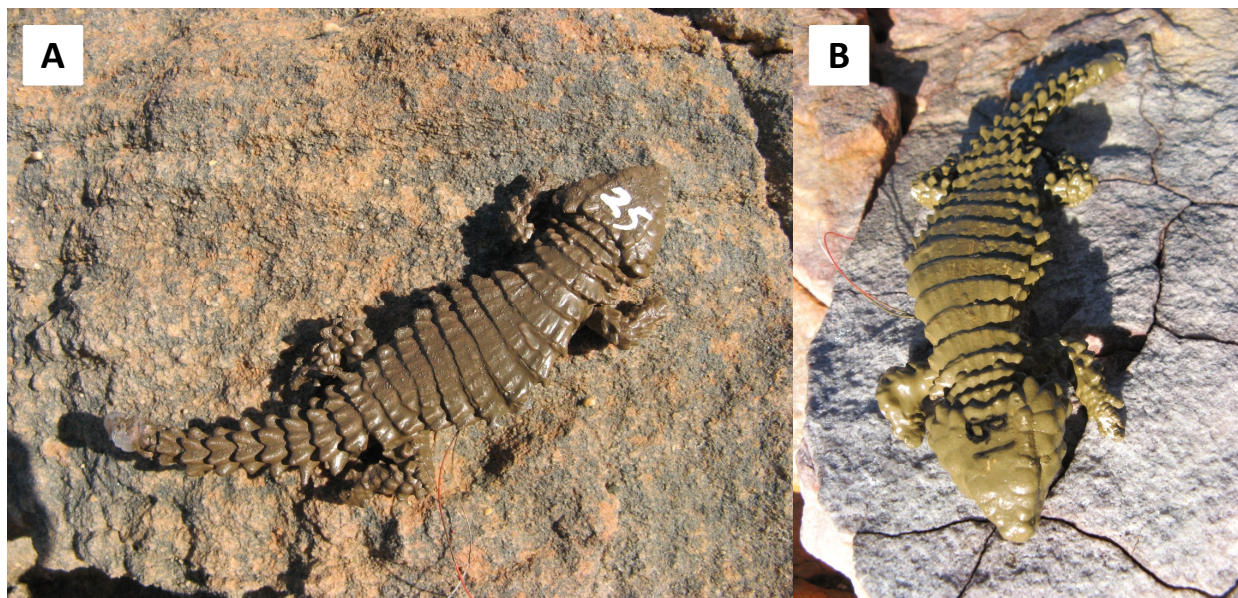

Figure 4.2. Hollow copper models of *C. cataphractus* painted in accordance to the skin absorbance of an Elands Bay (A) and Matjiesriver (B) population measured at 250 to 2500nm.

In order to select appropriate paint, the initial skin reflectance of one individual per population was measured with a USB 5000 spectroreflectometer (Ocean Optics, USA) at 300 nm to 750 nm. To calculate a mean reflectance through the spectrum, measurements were taken at 40 random points across each animal's body surface. The same device was then used to identify paints that match the mean reflectance. The skin reflectance of one lizard per population was subsequently measured at 250 nm to 2500 nm (to include a larger portion of the IR spectrum) with a Lambda 90 UV/VIS spectroreflectometer (Perkin Elmer, USA). This device has a refraction sphere that integrates reflectivity over a surface area of ~2500.0 mm^2. Three measurements were taken on the dorsal body surface of each lizard. The integrated reflection values taken at each location was averaged, providing an average reflection value for the individual to represent the particular population (Figure 4.3).

After noting a considerable difference between the average reflective values measured at 300 nm – 750 nm (coastal population: 21.7 % ± 14.6 %; inland population: 46.4 % ± 24.7 %), and 250 nm – 2500 nm (coastal: 14.3 % ± 9.0 %; inland: 17.9 % ± 10.2 %), models were re-painted prior to the spring field trial, since the autumn trial had already been completed. Colour and hue space values from the 250 nm – 2500 nm range of reflective values were determined and translated to blue, red and yellow colour and hue parameters, which were used as reference values to compose paint-colours that accurately match the average (integrated) reflectances of the lizards (i.e. coastal: DCB 432 Dark brown; inland: DSE 546 Sahara green, Plascon, RSA).
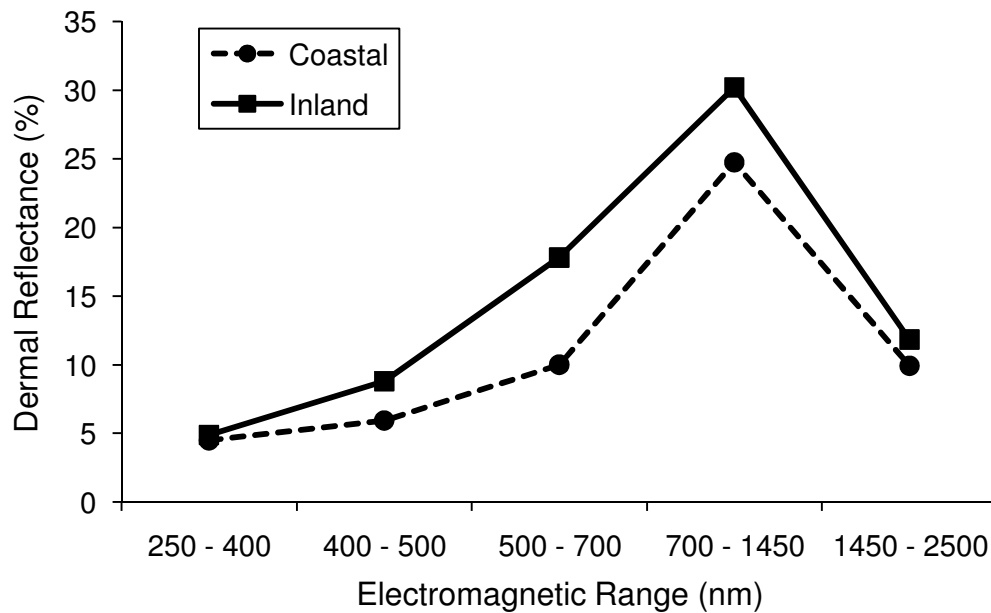
Figure 4.3. The mean skin reflectances recorded for a coastal and inland population of *C. cataphractus*. Measurements were taken with a Lambda 90 UV/VIS spectrometer (Perkin Elmer, USA). Values represent the major means of measurements taken (at three positions on the dorsal body surface of each lizard) at five nanometre intervals across a 250 nm to 2500 nm range (*N* = one lizard per population).

Each T_e-model was fitted (internally) with an iButton temperature logger (Maxim, USA). Models were initially filled with water (to mimic animal tissue) (first field trial, autumn, 2008), but had a low success rate due to extensive iButton failure and leakage of water. All models were therefore used empty (dry) during the subsequent (spring) trial. The T_e-models from the autumn trial were categorized based on their water content when collected (i.e. 0 %, 50 % or 100 % water content). Four combinations of T_e models were therefore used in this study (i.e. three in autumn according to reflection measurements in the 300 nm – 750 nm range, and one for spring according to the 250 nm – 2500 nm reflection range). Measurements taken with each model-type were adjusted according to the appropriate linear regression function (see section 4.3.2.2).

4.3.2.2 Model validation and calibration

The heat responses of models and live lizards were compared to obtain the correlation between operative temperatures (T_es) and real equilibrium body temperatures (T_b) of a live lizard. This linear regression function was used to adjust T_e values.

A single lizard from each population was fitted with a K-type thermocouple secured ~10 mm into its cloaca with strips of adhesive tape (Elastoplast, UK). Each lizard was fixed firmly to a low thermally conductive cardboard sheet with plastic coated copper wire and placed beneath a halogen lamp (500 watts) alongside three T_e-models. All validations were done in a controlled environmental chamber (18 ^{o}C ± 1.5 ^{o}C). The halogen lamp was raised, allowing models and lizards to reach equilibrium temperatures, before being lowered at various intervals, thus generating a series of equilibrium temperatures which could be recorded with a Pico TC-08 data logger (Pico Technology, UK).

The measure of correlation between lizard and T_e-model temperatures was assessed with a linear regression (Figure 4.4). Theoretically, a slope of one and an intercept of zero indicate a perfect correlation between model and lizard equilibrium temperatures, therefore implying that the model paint colour represent the correct reflectance. All model temperatures (T_e) were calibrated according to the appropriate linear function (T_e = slope*T_b + y-intercept) for analyses purposes (Figure 4.4).
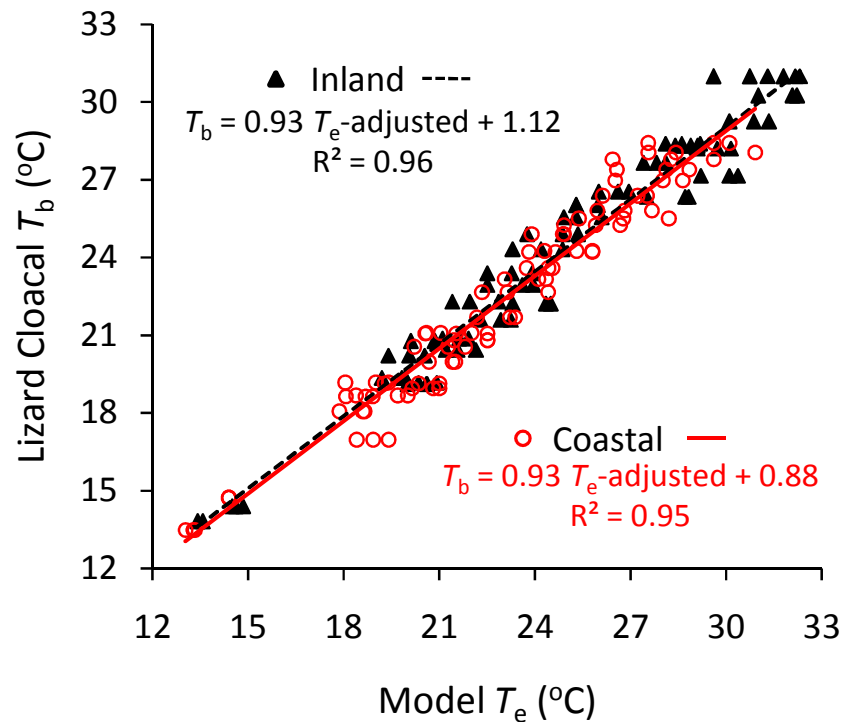
Figure 4.4. Two linear regression-fits indicating the correlation between lizard body temperatures (T_b-cloacal) and T_e-model temperatures (T_e) for both the coastal and inland populations of *C. cataphractus*. Models were painted as to match skin reflectance of live lizards, determined at 250 nm – 2500 nm. Individual readings represent equilibrium temperatures recorded beneath a 500W halogen bulb positioned at varying heights (N = one lizard and three models per population).

4.3.2.3 Model placement in the field (mapping the thermal environment)

Operative models were spread among rock-aspects (representing the four main wind directions, NESW) of a subset of rocks corresponding to those typically inhabited by *C. cataphractus* (coastal: N = eight rocks, 34 models; inland: N = nine rocks, 22 models). This approach was specifically followed to, in theory, map the thermal habitat around a single hypothetical rock, and in the process prevent pseudo replication through the oversampling of a limited number of rocks (Hurlbert 1984). A minimum of five models were collectively placed within or on the edges of crevices, whereas the rest were placed at variable distances away from crevices. Operative environmental temperatures (T_e) were recorded at the two localities

in concert at 15 minute intervals during April (autumn) and September (spring) for 14 consecutive days.

4.3.3 Field body temperatures (T_b)

Effectiveness and cost of thermoregulation can only be assessed if data on body temperatures of free ranging lizards are available (Hertz *et al.* 1993). Field body temperatures (T_b) for *C. cataphractus* individuals were recorded with Thermochron iButton temperature loggers (Maxim, USA), physically modified as illustrated by Robert and Thompson (2003) (Figure 4.5). The electronic components panel and battery were arranged alongside each-other which further reduce the thickness of the logger to 3.8mm. The loggers were waterproofed with Plastidip (Performix, USA) and attached to the dorsal body surface of the lizard using super glue gel (Henkel Pattex, DE).

Although reports of inter-group movements exist (Costandius *et al.* 2006), *Cordylus cataphractus*, in most cases, inhabit a single rock for prolonged periods (Visagie 2001; Effenberger and Mouton 2007), making it practical to attach micro-temperature-loggers to these animals without the use tracking equipment. However, during extended periods of field recording, loss of lizards (due to emigration or death) is a reality.

All iButtons were calibrated using the equations derived from linear regression of body surface temperatures versus cloacal-T_bs for individuals from the respective populations (see section 2.3.2.2); therefore, partly correcting for the difference between the actual internal T_b and body surface temperature. Field body temperatures (T_b) were recorded in concert with T_e at 15 minute intervals for 14 days during April (autumn) and September (spring) 2008.

Figure 4.5. A *Cordylus cataphractus* individual from the inland Matjiesriver population fitted with a modified Thermochron iButton temperature logger. The lizard is positioned in front of a rock crevice characteristically inhabited by the species.

4.3.4 Preferred temperature range (T_p)

The preferred temperature ranges (T_p) of both the inland and coastal populations were estimated in a laboratory thermal gradient during the autumn and spring of 2008 (Chapter 2).

4.3.5 Data analysis

4.3.5.1 Calculation of thermoregulatory indices

The indices describing thermal habitat quality (d_e), accuracy of thermoregulation (d_b) (Hertz *et al.* 1993), the effectiveness of thermoregulation ($d_e - d_b$) (Blouin-Demers and Weatherhead 2001) and thermal exploitation (E_x) (Christian and Weavers 1996) were calculated by selectively employing T_e, T_b and T_p (see section 3.3.5.1).

4.3.5.2 Statistical analysis

Rainy, overcast or abnormally windy days were excluded as well as days when a subset of lizards clearly remained inactive (having markedly lower T_bs than the others on a specific day), leaving nine clear skies days in autumn and four in spring. The data from several models were lost due to either iButton failure or T_e-models that were damaged, moved, or carried off by wild and/or domestic animals (autumn: N = 21 coastal and nine inland; spring N = 28 coastal and 21 inland). Similarly, the data of numerous lizards were lost due to either faulty iButtons, or irretrievable individuals (autumn: N = seven coastal and four inland; spring N = three coastal and three inland).

Temporal autocorrelation of data was assessed with Time Series Analysis (STATISTICA 8, Statsoft Inc., USA). Typically, temperatures taken 30 minutes apart were independent of each other for both T_e and T_b. Normality of data was assessed with the Shapiro-Wilk's W-test or Kolmorokov-Smirnhof when datasets exceeded 2000 values. Transformations did not improve normality and was subsequently not used.

Because of the nature of the data (being both repeated measures across days, unbalanced due to missing values and since residuals were in many cases not normally distributed) generalized linear mixed model analyses (PROC GLIMMIX, SAS Institute Inc., USA) with experimental day as repeated measure were used. The compound symmetry covariance structure was employed (Littell *et al.* 1996). The analysis was performed on hourly means calculated from measurements taken at 15 minute intervals (7h00 – 19h00) leaving 12 hourly mean values per day per season for each experimental unit (i.e. model or lizard). Although some of the lizards were used during more than one season, these were in the minority and lizards were therefore assumed as independent among seasons.

A non-parametric bootstrap ANOVA (x1000 iterations) (Efron 1993) (performed on hourly means calculated per season for each lizard unit) was applied for the thermal exploitation index (E_x) since the index was calculated across days and therefore lacks "experimental day" as repeated measure. Gender had no significant effect on T_b or d_b during all four seasons (P > 0.95) and was subsequently excluded from all analyses. Data were

analyzed using SAS Enterprize Guide 3, SAS 9.1 (SAS Institute Inc., USA) and STATISTICA 8 (Statsoft Inc., USA). Means are reported ± one standard deviation (SD). Probability values (P) of less than 0.05 were accepted as significant.

4.4 Results

4.4.1 Operative T_e-model calibration

The models from the coastal population (0 %, 50 % and 100 % water volume) were highly correlated to lizard T_b, with slopes close to one and y-intercepts relatively close to zero in all three cases (0 % (water content): T_e-adjusted = 0.96 T_b − 0.04, R² = 0.93; 50 %: T_e-adjusted = 1.02 T_b − 1.12, R² = 0.95; 100 %: T_e-adjusted = 1.02 T_b − 0.50, R² = 0.97). In contrast, the inland population's models were less accurate representations of live lizards (0%: T_e-adjusted = 0.85 T_b + 0.75, R² = 0.82; 50 %: T_e-adjusted = 0.68 T_b + 6.28, R² = 0.94; 100 %: T_e-adjusted = 0.91 T_b + 0.16, R² = 0.96). The models of both populations that were repainted according to 250 nm – 2500 nm reflectance values were more accurate than those based on the initial 300 nm – 750 nm reflectivities, with slopes and intercepts of close to one and zero (coastal: T_e-adjusted = 1.02 T_b + 0.24, R² = 0.95; inland: T_e-adjusted = 1.03 T_b − 0.10, R² = 0.96) (Figure 4.4). The slopes differed significantly from zero for all model types (P < 0.01). Model temperatures did not vary significantly from lizard body temperatures (T_b) (when exposed to equal radiation) in all cases at both the coastal (300 nm – 750 nm: 0 % (water content), P = 0.33; 50 %, P = 0.53; 100 %, P = 0.89; 250 nm – 2500 nm, P = 0.29) and inland populations (250 nm – 750 nm: 0%, P = 0.06; 100%, P = 0.14; 250 nm – 2500 nm, P = 0.35), except for the inland 50 % water content model (P = 0.02) (non-parametric bootstrap ANOVA).
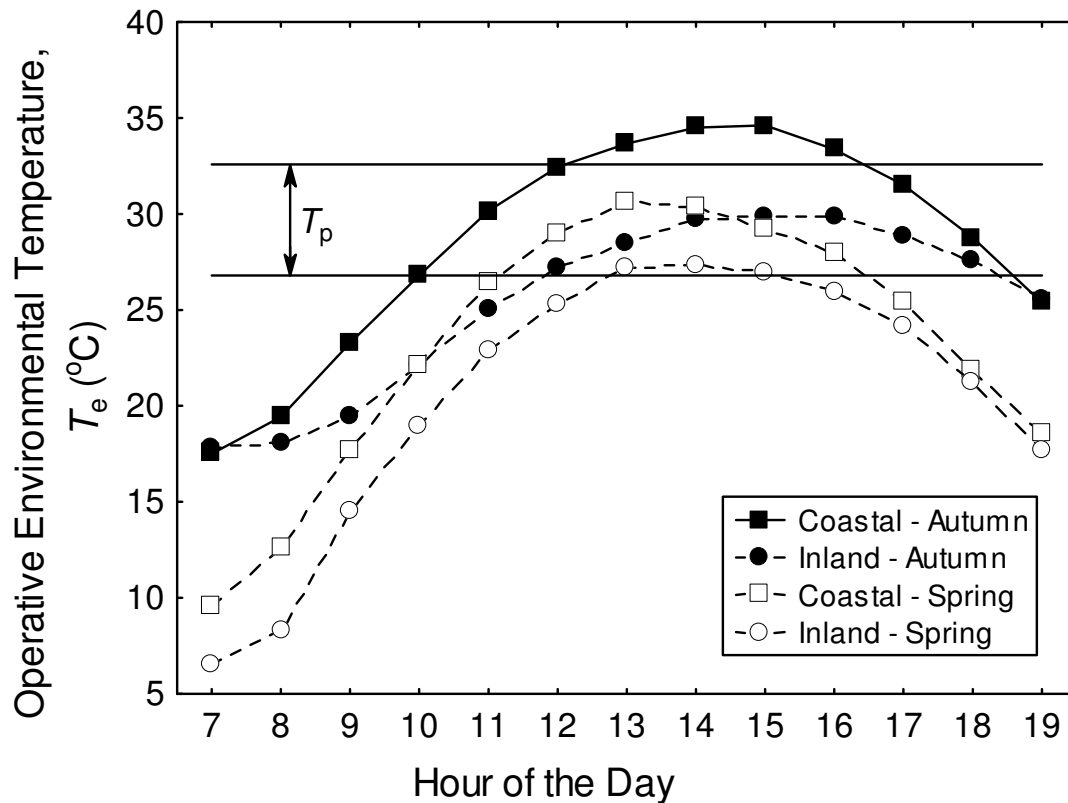
Figure 4.6. Mean operative environmental temperatures (T_e) as a function of the time of the day, at a coastal and inland population of *C. cataphractus* during autumn and spring (calculated across sample days; N = nine autumn days, five spring days). The horizontal rectangle depicts the preferred temperature range of *C. cataphractus*.

4.4.2 Spatial and temporal variation in operative environmental temperatures (T_e) and thermal habitat quality (d_e) (Figures 4.6, 4.7, 4.8 and 4.9)

Mean operative environmental temperatures (T_e) varied significantly as a function of the time of day ($F_{11,858}$ = 605.54, P < 0.01), time of year (season) ($F_{1,75}$ = 23.14, P < 0.01) and geographic location (population) ($F_{1,75}$ = 13.86, P < 0.01). Moreover, mean T_es were significantly higher in autumn than spring at both localities (coastal: $F_{1,47}$ = 14.18, P < 0.01; inland: $F_{1,28}$ = 12.22, P < 0.01) (Figure 4.6; Table 4.2), resulting in varied thermal habitat quality (d_e), being significantly lower (high d_e) in the cooler spring than autumn at both populations (inland: $F_{1,28}$ = 30.57, P < 0.01; coastal: $F_{1,47}$ = 37.71, P < 0.01) (Figures 4.6 and 4.7; Table 4.2). The proportion of T_es within T_p was 49.2 % at the inland and 31.2 % at the

coastal locality during autumn, compared to the respective 22.8 % and 13.4 % in spring (7h00 – 19h00) (Figures 4.8 and 4.9).

In autumn, the inland locality had favourable T_es (overall mean T_e = 26.0 ^{o}C), on average matching T_p from 12h00 to 18h00 (Figure 4.6), and resultingly high thermal habitat quality (d_e approaching zero) (overall mean d_e = 2.0 ^{o}C) (Figure 4.7). Conversely, mean T_es at the coastal locality only matched T_p from 10h00 to 12h00 and again from 17h00 to 18h00 in autumn (Figure 4.6), generally being higher (overall mean T_e = 29.5 ^{o}C; $F_{1,28}$ = 9.29, $P <$ 0.01) and significantly less favourable (i.e. low thermal habitat quality) than that of the inland locality (overall mean d_e = 3.3 ^{o}C ± 3.8 ^{o}C; $F_{1,28}$ = 9.3, $P <$ 0.01) (Figure 4.7).

In spring, T_es were unfavourable at the inland locality (overall mean T_e = 21.7 ^{o}C), on average matching T_p only from 13h00 to 15h00 (Figure 4.6) which related to generally poor thermal quality (high deviation of T_e from T_p) (overall mean d_e = 6.3 ^{o}C). The coastal locality had significantly higher mean T_es than the inland during spring (overall mean T_e = 24.3 ^{o}C; $F_{1,47}$ = 9.64, $P <$ 0.01). Conversely, although mean T_e equalled T_p for at least two hours longer at the coastal locality (12h00 – 16h00) (Figure 4.6), the overall thermal habitat quality (d_e) (7h00 – 19h00) was still low (high d_e) (overall mean d_e = 6.6 ^{o}C), and did not vary significantly from that of the inland locality ($F_{1,47}$ = 0.03, P = 0.87) (Figure 4.7).

Table 4.2. Summary of the overall mean operative temperatures (T_e), field body temperatures (T_b), preferred temperature range (T_p), thermal habitat quality (d_e), accuracy of thermoregulation (d_b), effectiveness of thermoregulation ($d_e - d_b$) and % thermal exploitation (E_x) measured and calculated respectively for a coastal and inland population of *C. cataphractus* during autumn and spring.

Population	Season	Time	T_e (°C)	T_b (°C)	T_p (°C)	d_e (°C)	d_b (°C)	$d_e - d_b$*	E_x (%) (10h00-18h00)
Coastal	Autumn	7h00 – 19h00	29.5 ± 7.5	27.0 ± 4.2	26.3-33.0	3.3 ± 3.8	1.6 ± 2.2	2.0 ± 1.9	58.5 ± 33.8
		24h	24.7 ± 7.7	26.0 ± 3.7		4.9 ± 4.1	1.8 ± 2.1	3.2 ± 2.2	
	Spring	7h00 – 19h00	24.3 ± 9.0	24.9 ± 8.2	27.5-32.6	6.6 ± 5.6	5.1 ± 5.9	2.6 ± 2.1	39.7 ± 18.6
		24h	18.2 ± 9.3	20.4 ± 7.8		11.0 ± 6.5	8.4 ± 6.0	3.2 ± 1.9	
Inland	Autumn	7h00 – 19h00	26.0 ± 4.8	27.1 ± 4.7	25.8-32.5	2.0 ± 2.9	1.6 ± 2.5	0.8 ± 1.3	56.8 ± 30.5
		24h	23.1 ± 4.7	25.8 ± 4.5		3.8 ± 3.2	1.9 ± 2.8	2.1 ± 2.0	
	Spring	7h00 – 19h00	21.70 ± 7.9	21.2 ± 8.0	26.6-32.6	6.3 ± 6.3	6.7 ± 6.4	1.6 ± 2.0	19.3 ± 19.3
		24h	15.9 ± 8.6	18.2 ± 6.9		11.4 ± 7.4	9.0 ± 5.7	3.2 ± 2.7	

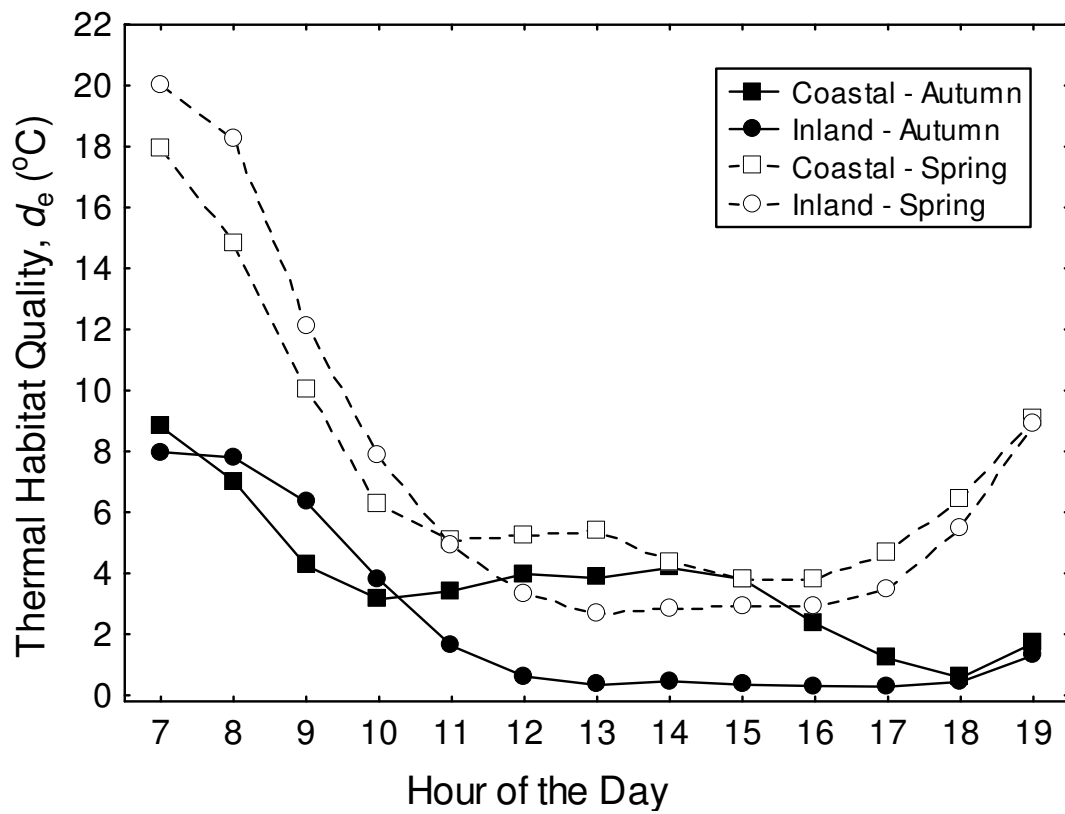*Calculated only from positive $d_e - d_b$ (see section 4.4.4)

Figure 4.7. Thermal habitat quality (d_e) calculated for a coastal and inland population of *C. cataphractus* during autumn and spring. A low d_e indicates high thermal quality (i.e. small difference between T_e and T_p).

Figure 4.8. The frequency distributions of operative environmental temperatures (T_e) and field body temperatures (T_b) recorded in a coastal and inland population of *C. cataphractus* during autumn. Arrow heads indicate overall means, whereas the vertical rectangle depicts the preferred temperature range of *C. cataphractus* as determined for the respective populations during autumn (T_e: N = 21 operative models coastal and nine inland; T_b: N = seven lizards coastal and four inland).
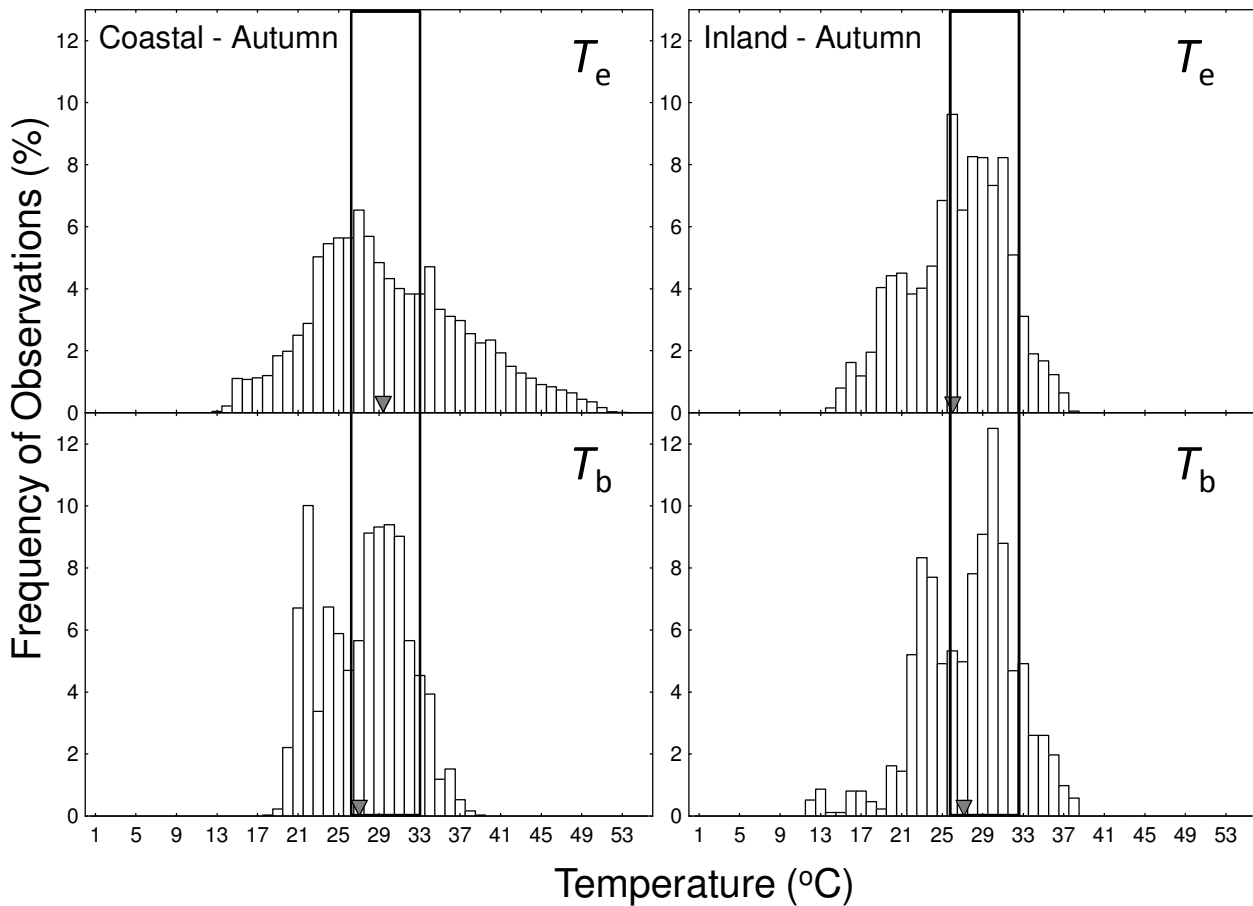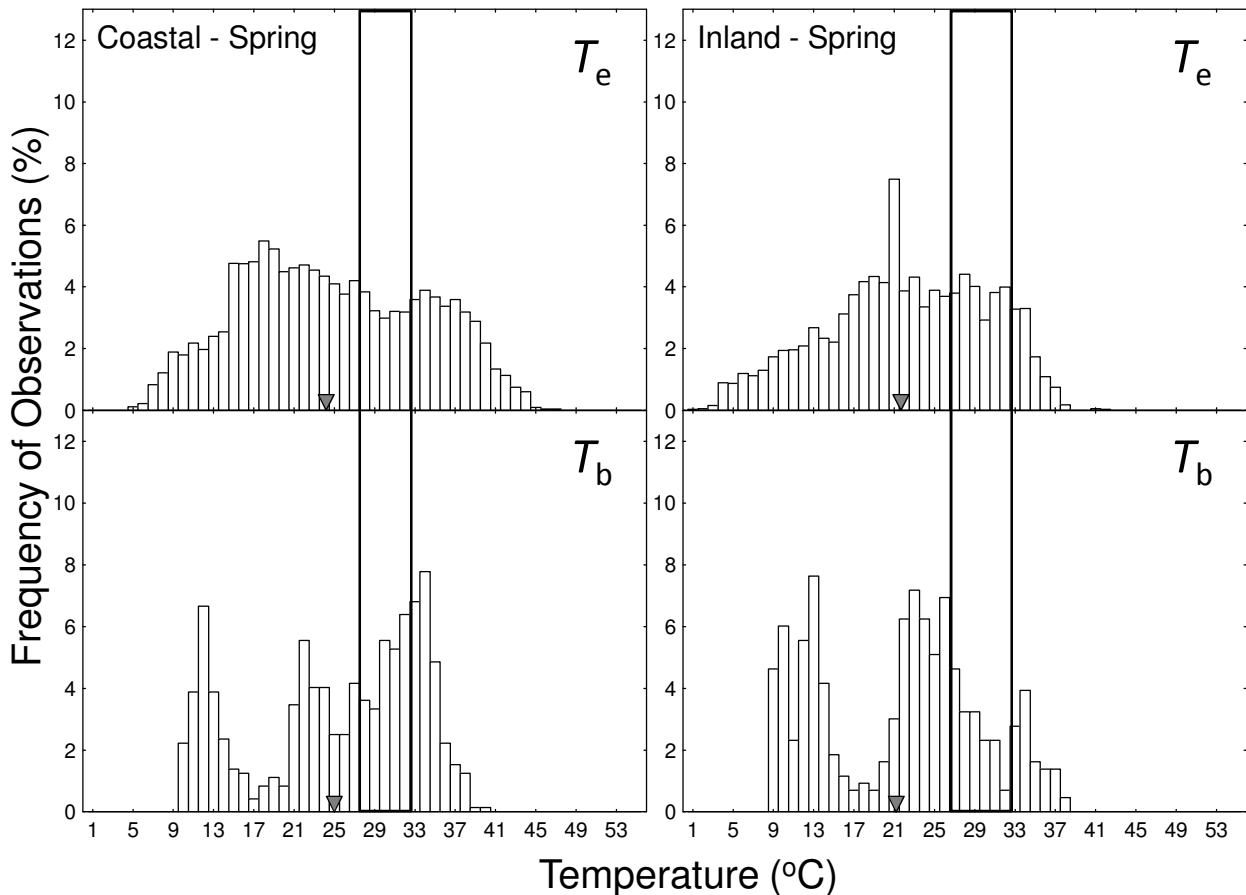
Figure 4.9. The frequency distributions of operative environmental temperatures (T_e) and field body temperatures (T_b) recorded during spring (7h00 – 19h00) in a coastal and inland population of *C. cataphractus*. Arrow heads indicate overall means, whereas the vertical rectangles depict the preferred temperature range of *C. cataphractus* as determined for the respective populations during spring (T_e: N = 28 models coastal, 21 inland; T_b: N = three lizards coastal, three inland).

4.4.3 Field body temperatures (T_b) and accuracy of thermoregulation (d_b) (Figures 4.8, 4.9, 4.10 and 4.11)

Mean field body temperatures (T_b) varied significantly as a function of the time of day ($F_{8,98}$ = 20.07, P < 0.01), time of year (season) ($F_{1,13}$ = 41.39, P < 0.01) and geographic location (among populations) ($F_{1,13}$ = 11.54, P < 0.01). The inland population maintained significantly higher mean T_bs during autumn than spring (overall means: autumn 27.1 °C ± 4.7 °C, spring 21.2 °C ± 8.0 °C; $F_{1,5}$ = 308.19, P < 0.01) (Figure 4.10), which corresponds to the trend

observed in T_e (Figure 4.6). The T_bs of the coastal population, although on average being higher in autumn than spring, did not vary significantly among seasons (overall means: autumn 27.0 ^{o}C ± 4.2 ^{o}C; spring 24.9 ^{o}C ± 4.7 ^{o}C; $F_{1,8}$ = 2.08, P = 0.19) (Figure 4.10; Table 4.2), in contrast to the trend observed in T_e (Figure 4.6). The higher autumn-T_bs related to significantly higher mean thermoregulatory accuracy (low d_b) (T_bs approaching T_p) than spring at both the coastal ($F_{1,8}$ = 59.32, P < 0.01) and inland ($F_{1,5}$ = 467.33, P < 0.01) populations (Figure 4.11; Table 4.2). Moreover, the proportion of T_bs within T_p was higher at both populations in autumn (inland: 50.2%; coastal: 50.7%) than in spring (inland: 29.4%; coastal: 15.5%) (7h00 – 19h00) (Figures 4.8 and 4.9).

Autumn was characterized by the accurate maintenance of T_b within T_p (low d_b) at both populations (overall mean d_b: coastal 1.6 ^{o}C ± 2.2 ^{o}C; inland 1.6 ^{o}C ± 2.5 ^{o}C) for prolonged periods (coastal: 13h00 – 22h00; inland 12h00 – 23h00) (Figures 4.10 and 4.11). Conversely, during spring, thermoregulatory accuracy was low (overall mean d_b: coastal 5.1 ^{o}C ± 5.9 ^{o}C; inland 6.7 ^{o}C ± 6.4 ^{o}C) and mean T_bs equalled T_p for shorter periods (coastal: 12h00 – 17h00; inland: 14h00 – 17h00) (Figures 4.10 and 4.11).

At geographic scale, mean field body temperatures (T_b) varied significantly among populations during spring ($F_{1,4}$ = 11.93, P = 0.03), being higher and closer to T_p in the coastal population (i.e. significantly lower d_b: $F_{1,4}$ = 9.09, P = 0.04) (Figures 4.10 and 4.11; Table 4.2). Conversely, during autumn, both mean T_b and mean d_b did not vary significantly among populations (T_b: $F_{1,9}$ = 0.17, P = 0.69; d_b: $F_{1,9}$ = 0.15, P = 0.71) (Figures 4.10 and 4.11).
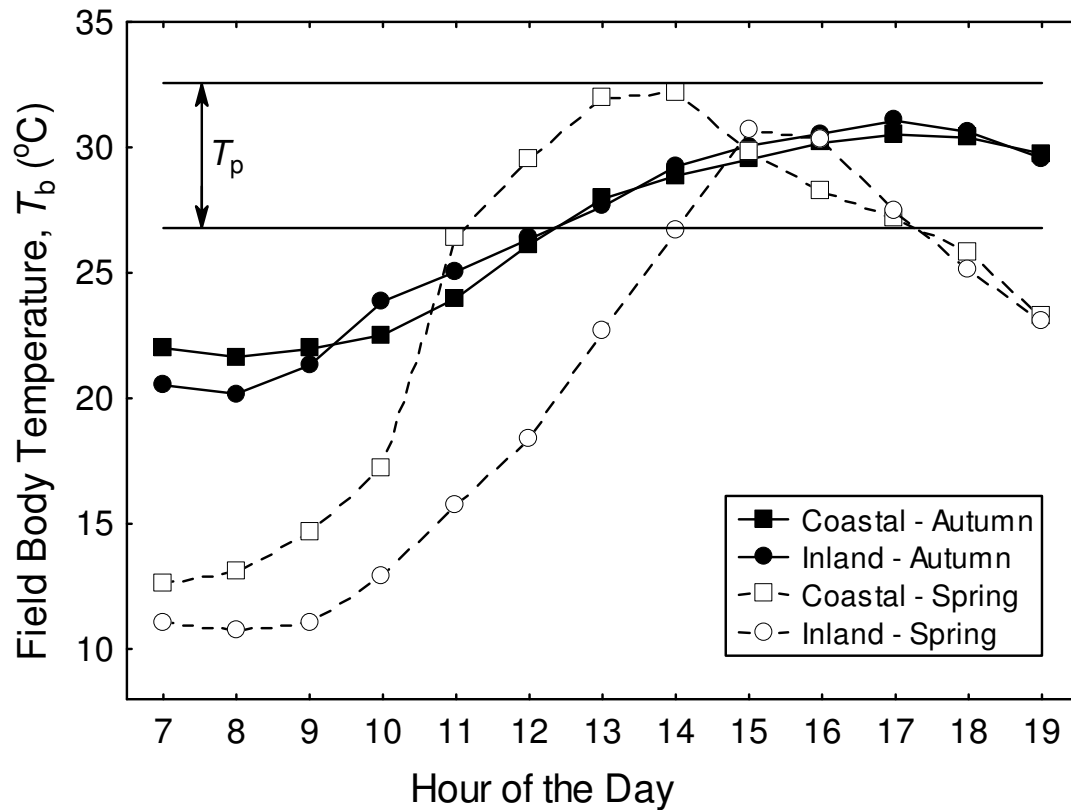
Figure 4.10. Mean field body temperature (T_b) as a function of time of day in a coastal and inland population of *C. cataphractus* during autumn and spring. The horizontal lines depict the preferred temperature range of *C. cataphractus.*
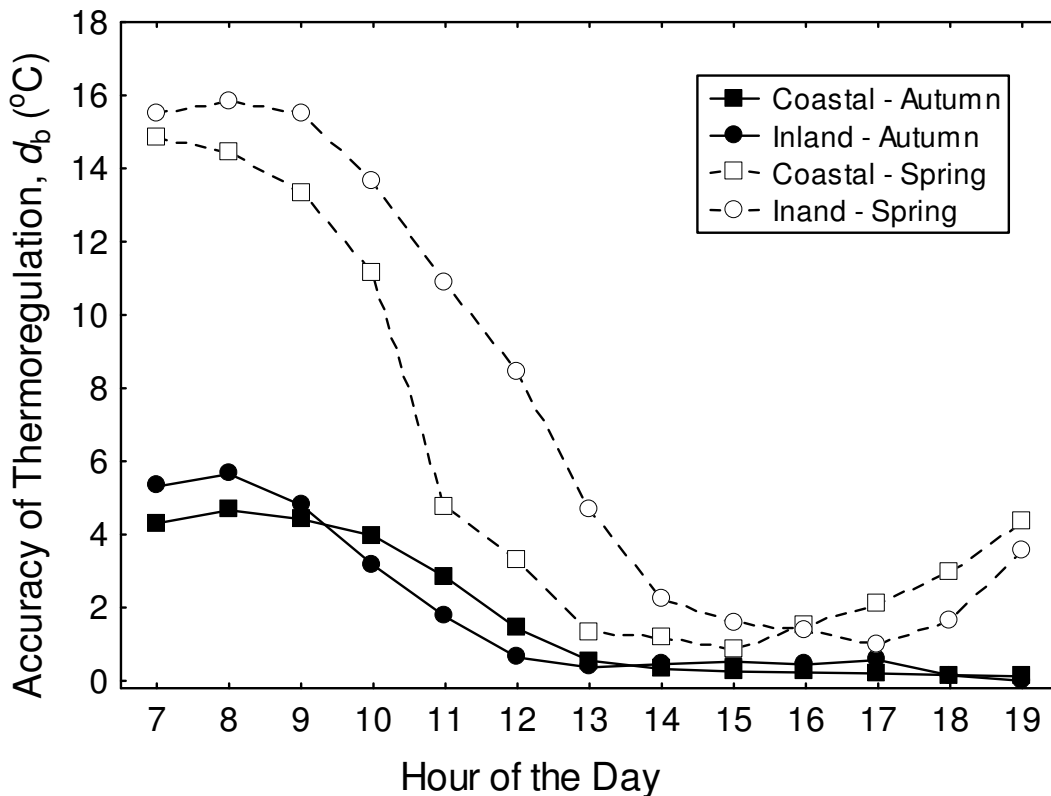
Figure 4.11. Accuracy of thermoregulation (d_b), expressed as the degree of deviation of T_b from T_p, as a function of time of day in a coastal and inland population of *C. cataphractus* during autumn and spring. A d_b value of zero indicates perfect accuracy (i.e. $T_b = T_p$) (Hertz *et al.* 1993).

4.4.4 Effectiveness of thermoregulation ($d_e - d_b$) and thermoregulatory strategy (thermoregulation versus thermoconformation) (Figures 4.12 and 4.13)

A high frequency of $d_e - d_b$ values were below zero at both populations during spring (Figure 4.12), suggesting avoidance of thermally suitable microhabitats (Hertz *et al.* 1993; Blouin-Demers and Weatherhead 2002). For analysis purposes, all $d_e - d_b$ values below zero were subsequently transformed to zero, seeing that zero denotes perfect thermoconformation and sub-zero values would have an unrealistic influence on results from a thermoregulatory perspective.

Spring mean $d_e - d_b$ values were below zero for the majority of the day at the inland population (9h00 – 13h00), as well as (although for a shorter duration) at the coastal (9h00 – 10h00) (see Figure 4.12). Conversely, in autumn, mean $d_e - d_b$s were predominantly positive

at both populations, decreasing only slightly below zero at 10h00 in the coastal population, after which it gradually increased indicating active thermoregulation (Figure 4.12). Mean $d_e - d_b$s remained near zero for most of activity time in the inland population indicating thermoconformation (Figure 4.12).

The mean effectiveness of thermoregulation ($d_e - d_b$) differed significantly among seasons at the coastal ($F_{1,8} = 7.03$, $P = 0.03$) and inland ($F_{1,5} = 107$, $P < 0.01$) populations (Figure 4.12; Table 4.2). At geographic scale, the mean effectiveness of thermoregulation ($d_e - d_b$) was significantly higher at the coastal than inland population during autumn ($F_{1,9} = 210.27$, $P < 0.01$), yet not during spring ($F_{1,4} = 7.18$, $P = 0.06$) (Figure 4.12; Table 4.2).

Figure 4.12. The effectiveness of thermoregulation ($d_e - d_b$) which expresses the degree of departure from thermoconformity ($d_e - d_b = 0$: perfect thermoconformity), as a function of time of day in a coastal and inland population of *C. cataphractus* during autumn and spring.
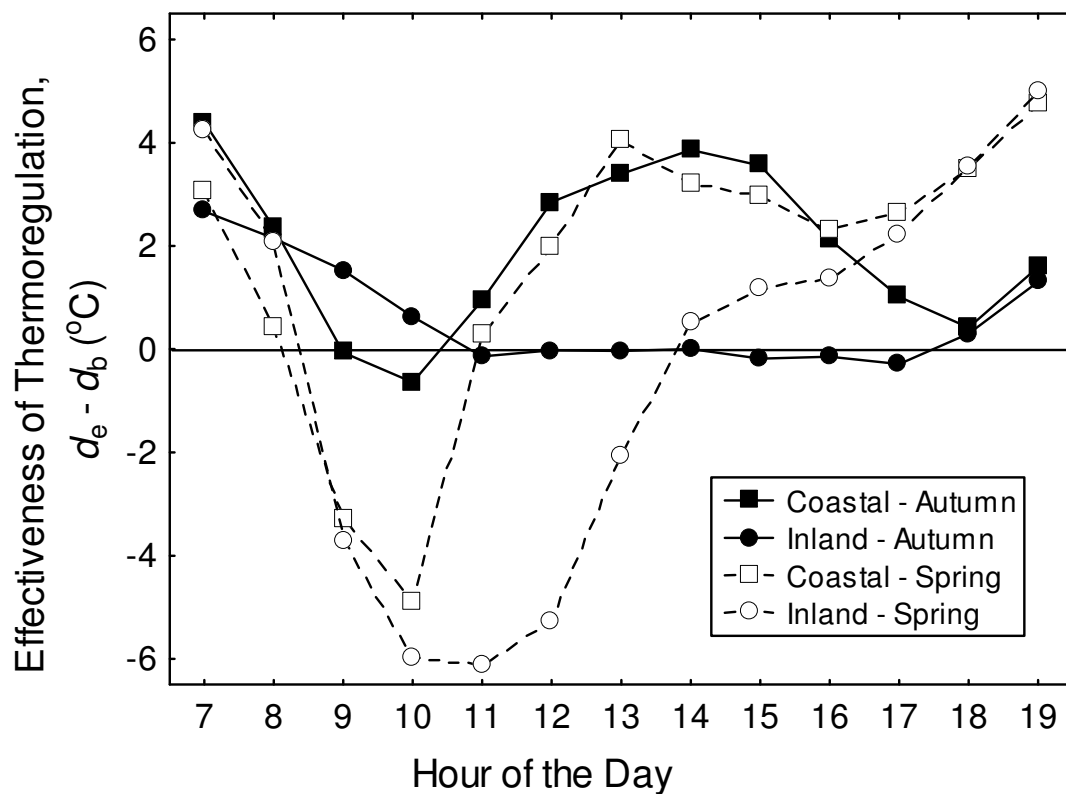
The correlation between thermal habitat quality (d_e) and the accuracy of thermoregulation (d_b) (Figure 4.13) provides a further estimate of thermoregulatory investment (Blouin-Demers and Nadeau 2005; Edwards and Blouin-Demers 2007), additionally categorizing investment in three groups based on the slope (m) of the correlation function: (1) a slope (m) = 1 indicates thermoconformity (the accuracy of thermoregulation therefore increasing or decreasing directly proportional to thermal habitat quality (see Figure 4.13)); (2) $m < 1$ suggests a decrease in thermoregulatory investment functional to increased thermal habitat quality (towards zero) (indicated by the vertical distance between thermoconformity slope (=1) and the data point) as predicted by the cost-benefit model of thermoregulation, since thermal habitat quality is the major determinant of thermoregulatory costs (Huey and Slatkin 1976); and (3) $m > 1$ increased thermoregulatory investment functional to decreased thermal habitat quality (i.e. increased costs).

In autumn, both populations moved further from conformity as thermal habitat quality became poorer which suggests active thermoregulation (i.e. thermoregulatory accuracy increased as thermal habitat quality decreased) (Figure 4.13). In spring, the coastal population moved towards conformity as thermal quality decreased, whereas the inland population seemed to tend towards thermoconformation across the d_e range (Figure 4.13).
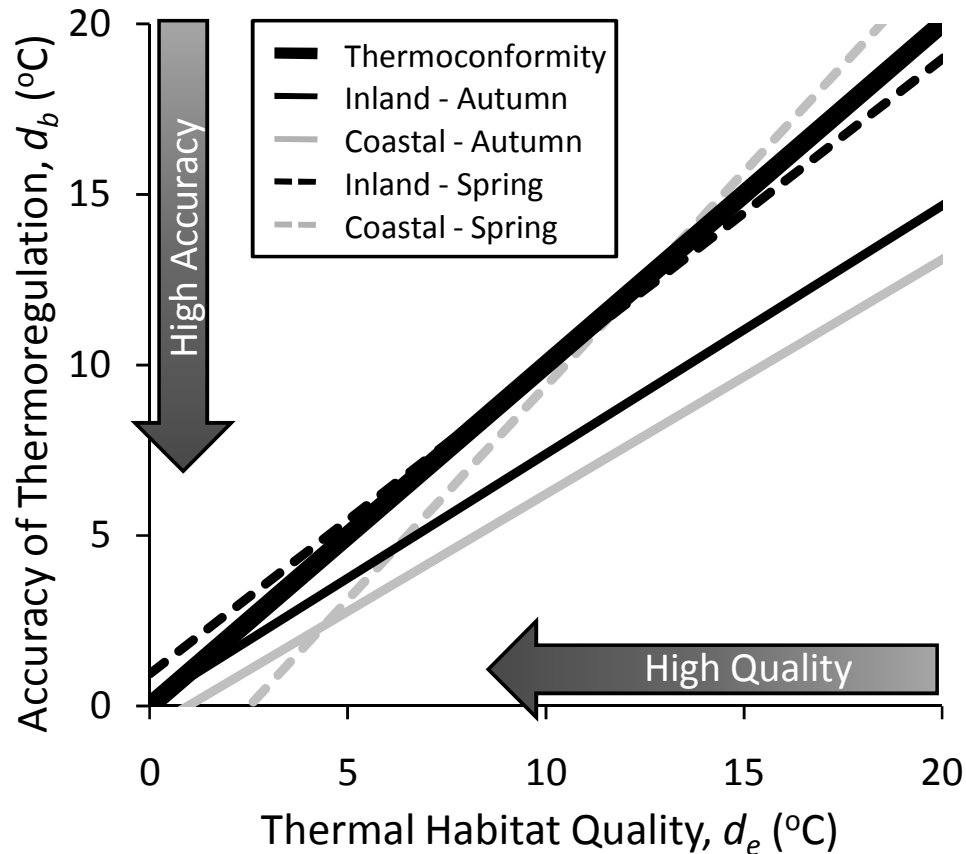
Figure 4.13. The accuracy of thermoregulation (d_b) (absolute deviation of T_b from T_p) versus thermal habitat quality (d_e) (the absolute deviation of T_e from T_p) in an inland and coastal population of *C. cataphractus* during autumn and spring. The solid black line represents thermoconformity (i.e. slope (m) = one). The vertical distance between the conformity line and a line representing a particular species/population indicates effectiveness of thermoregulation ($d_e − d_b$) (Blouin-Demers and Nadeau 2005). The cost-benefit model of thermoregulation (Huey and Slatkin 1976) predicts that the accuracy of thermoregulation will increase (i.e. decreased d_b) proportional to increased thermal habitat quality (i.e. decreased d_e) resulting in a slope which exceeds one ($m > 1$). In autumn, lizards from both populations thermoregulated more effectively (described by $d_e − d_b$) when thermal habitat quality was low (coastal autumn, $m = 0.69$; inland autumn, $m = 0.73$; coastal spring, $m = 1.25$; inland spring, $m = 0.90$).

4.4.5 Thermal exploitation (E_x) (Figure 4.14)

The proficiency with which lizards exploited their thermal habitat (the time in which T_bs were within T_p divided by the time potential T_bs in T_p (i.e. T_e) were available) increased gradually as a function of time of day (as operative environmental temperatures (T_e) increased) at both localities during autumn and spring (Figure 4.14). In autumn, thermal exploitation was relatively high, exceeding 80 % for most of the afternoon at both the coastal (15h00 – 22h00) and inland populations (16h00 – 17h00 and 19h00 – 21h00) (Figure 4.14). Conversely, E_x was lower at both populations in spring than autumn. This difference was however significant only in the inland population (coastal: $P = 0.20$; inland: $P < 0.01$, non-parametric bootstrap ANOVA) (Figure 4.14; Table 4.2). At geographic scale, thermal exploitation was significantly higher at the coastal population in spring ($P < 0.01$, non-parametric bootstrap ANOVA) but not so in autumn ($P > 0.95$, non-parametric bootstrap ANOVA) (Figure 4.14; Table 4.2).

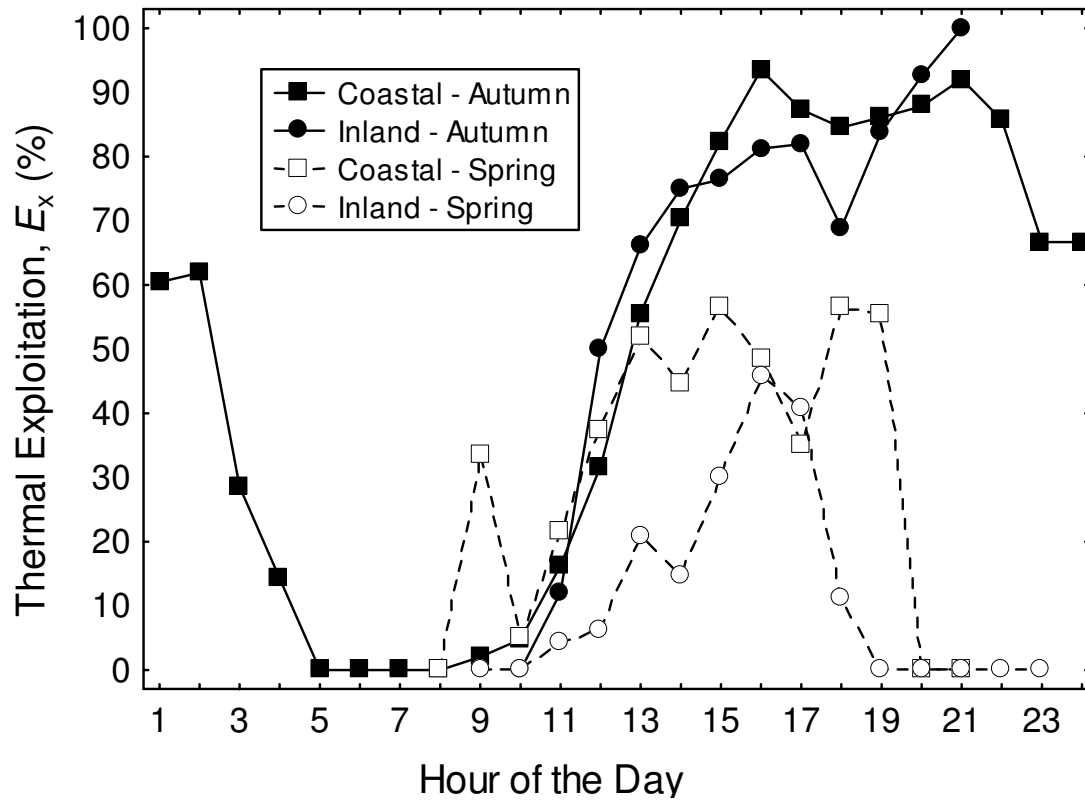Figure 4.14. Thermal exploitation (E_x) of a coastal and inland population of *C. cataphractus* as a function of time of day during autumn and spring. Thermal exploitation describes the degree to which a reptile exploits the thermally favourable opportunities for accurate thermoregulation, particularly describing the time-fraction (%) during which T_b equals T_p when permissive in a habitat (Christian and Weavers 1996).

4.5 Discussion

Ectotherms, characteristically exhibit low metabolic heat production with relatively low resistance to heat loss (Huey 1982). Behavioural and physiological thermoregulation is central to maintaining T_b within the preferred range of temperatures, the cost of which may be off-set by the benefit of increased/continued physiological performance (Angilletta 2009). The extent of thermoregulation in many reptilian species is known to vary temporally and geographically and may result in a total strategy change (from thermoregulator to thermoconformer) (Hertz *et al.* 1993; Schauble and Grigg 1998), or simply reduced thermoregulatory activity/investment (Angilletta 2001; Diaz and Cabezas-Diaz 2004; Clusella-Trullas *et al.* 2009).

The cost benefit model of thermoregulation (Huey and Slatkin 1976) attempts to explain thermoregulatory investment and implicitly states that the extent/effectiveness of behavioural thermoregulation performed varies as a function of the relative cost–to–benefit ratios of such behaviour, and that if the costs outweigh the benefits, thermoregulatory activity will be abandoned. In a recent meta analysis, Blouin-Demers and Nadeau (2005) explored the effectiveness of thermoregulation ($d_e - d_b$) and thermal exploitation (E_x) of numerous lizards from variable habitats and surprisingly observed a trend for lizards to invest more (i.e. higher $d_e - d_b$) in high cost habitats opposed to low cost habitats, in contrast to the prediction of the cost-benefit model of thermoregulation. The results of Blouin-Demers and Nadeau (2005) suggest that the disadvantages of thermoconformity outweigh the costs of thermoregulation in thermally unfavourable habitats.

Cordylus cataphractus exhibits various life history traits such as a sit-and-wait foraging mode (Mouton *et al*. 2000a), permanent group-living (Mouton *et al*. 1999), extended periods of lowered surface activity (Visagie 2001), a degree of thermally independent and highly repressed resting metabolic rate (RMR) (Mouton *et al*. 2000b), which makes this species an ideal model to answer questions regarding the cost-benefit model for thermoregulation. Moreover, this study is one of few studies addressing the functional thermal ecology of an

African reptile species, and the first to explore population-level variation in field thermal ecology.

In spring, the success and effectiveness of thermoregulation as well as the proficiency with which available favourable T_es in the habitat was exploited varied significantly among the inland and coastal populations, even though thermal habitat quality did not. Thermoregulatory success was higher in both the inland and coastal populations of *C. cataphractus* during the dry autumn (when the expected food constraints amplified by a group-living life strategy expectedly peaks (Mouton *et al.* 2000a)) than the more mesic spring when food abundance is high.

Hollow copper models of lizards have not been widely used in local thermoregulation studies (Clusella-Trullas *et al.* 2009), and the current results underline the value of using operative temperature (T_e)-models painted according to lizard dermal reflectance (EM spectrum range from UV to near IR, 2500nm) to obtain a view of the distribution of operative temperatures in a lizard's habitat. Dzialowski (2005) reviewed the use of operative temperature models and stressed the importance of painting models to closely match the animal's dermal absorbance as well as to calibrate such models. When model equilibrium temperatures are correlated to the equilibrium body temperatures of a live lizard exposed to matching thermal conditions, a slope and R^2 of one in the correlation function indicates that the model provides perfect representations of equilibrium T_bs. The current copper models provided more realistic equilibrium T_bs when painted in relation to a broader range of skin absorbance which includes a portion of the near infrared spectrum (i.e. 250 nm – 2500 nm), in comparison to a narrower range (300 nm – 750 nm), and in general were good representations of lizard equilibrium body temperatures.

Skin reflectance varied among populations, being 3.5 % higher at the inland (17.9 %) than the coastal (14.3 %) population (250 nm – 2500 nm). Published records of skin reflectance exist for only three other cordylids namely: *Cordylus cordylus* (15.2 %) and the melanistic *Cordylus niger* (5.3 %) and *Cordylus oelofseni* (6.9 %) (290 nm – 2600 nm)

(Clusella-Trullas *et al*. 2009). Measurements obtained for *C. cataphractus* corresponded closely to the non-melanisitic *C. cordylus* (Clusella-Trullas *et al*. 2009).

The modified Thermochron iButtons, although relatively unreliable because of low recapture success or electronic failure, still proved functional and valuable to measure field body temperatures (Robert and Thompson 2003; Lovegrove 2009). Modified iButtons therefore comprise a useful alternative to the conventional "grab and jab" or invasive radio telemetry techniques, allowing the continuous measurement of T_bs (Robert and Thompson 2003).

In spring, mean field body temperatures as well as thermoregulatory accuracy (d_b), effectiveness of thermoregulation ($d_e - d_b$) and thermal exploitation (E_x) varied significantly among populations despite the fact that thermal habitat quality (d_e) did not. In particular, mean body temperatures of individuals from the inland population on average reached the preferred temperature (T_p) range for only three hours per day (15h00 – 17h00), whereas the coastal population thermoregulated with higher accuracy, on average maintaining T_b within T_p for six hours per day (12h00 – 17h00). The thermal exploitation index (E_x) indicates that the inland population was less successful at maintaining T_b within T_p when permissive in their habitat in spring (E_x inland: 19.3%; coastal: 39.7%). Moreover, the effectiveness of thermoregulation ($d_e - d_b$) was higher at the coastal population. Note however that the mean $d_e - d_b$ values decreased below zero for a considerable period of time at the inland population (9h00 – 13h00) and for a shorter period at the coastal (9h00 – 10h00). A $d_e - d_b$ of zero describes thermoconformity and the magnitude of increase in $d_e - d_b$, the amount of thermoregulation performed (Blouin-Demers and Weatherhead 2001). Negative $d_e - d_b$ values may indicate active avoidance of thermally suitable microsites (Hertz *et al.* 1993; Blouin-Demers and Weatherhead 2001; Labra *et al.* 2001), and if variable among populations, is expected to result in differences in the effectiveness and success of thermoregulation.

Various potential sources of seasonal or geographic variation in thermoregulation correspond to that of avoidance behaviour (i.e. negative $d_e - d_b$s). These include: (1) social

behaviour such as mating and courtship (Shine 1980; Schauble and Grigg 1998; Herczeg *et al.* 2008); (2) predation risk (Hertz *et al.* 1993; Herczeg *et al.* 2008); (3) foraging behaviour (Hertz *et al.* 1993) and (4) territorial (home range) boundaries and aggression. In addition, the major known source of seasonal and geographical variation in thermoregulation is thermal habitat quality (Angilletta 2001; Blouin-Demers and Nadeau 2005), and an additional source of negative $d_e - d_b$s is operative models that are placed in micro habitats that are either inaccessible to the animals or inappropriate in relation to natural movement patterns (Wills and Beaupre 2000).

In an attempt to explain the variation in thermoregulation among the coastal and inland populations in spring, the abovementioned potential sources of variability in thermoregulation will be considered for geographic variation and negative $d_e - d_b$ values collectively seeing that these elements are most likely related.

(1) Social behaviour such as mating and courtship

Spring marks the beginning of the peak activity time and mating season of *C. cataphractus* (Visagie 2001). The avoidance of thermally suitable microsites or altered thermoregulation may be associated with mating and courtship (Shine 1980; Stevenson *et al.* 1985). Effenberger (2004) however reported that males and females respectively spent only 3.5 % and 2.2 % of the day exhibiting mating behaviour outside rock crevices during peak mating season and it therefore seems unlikely that social behaviour resulted in the observed geographic variation in thermoregulation.

(2) Territorial boundaries and aggression.

Large *C. cataphractus* groups may contain numerous males that typically occupy neighbouring sub-sections (around rocks) which they aggressively defend. Such territorial boundaries may deny males access to thermally suitable microsites. None of the groups sampled at the (low density) inland population however contained multiple males and the fact that the (negative $d_e - d_b$) effect was most pronounced at the inland population suggests male-male aggression as an unlikely explanation.

(3) Predation risk

2008). Hayward (2008) found that vigilance behaviour, scanning rate, predator detection rate and the tempo of re-emergence from crevices (after a potential predator encounter) proportionally decreases as a function of increased group size, thus providing conclusive evidence for predator evasion as a major advantage of the group-living life strategy in *C. cataphractus*. Group-living may therefore indirectly contribute to efficient thermoregulation due to reduced predation risk, which (in the context of *C. cataphractus*) is expected to occur in two ways. Firstly, the reduced vigilance and scanning rate associated with larger groups will relax time budgets, potentially allowing more time spent thermoregulating. Secondly, the lower vigilance and predator detection rate will promote movement (further) away from crevices which may improve thermoregulatory capacity. The aforementioned prediction is supported by the fact that individuals from larger groups are known to move further away from crevices in spring (Visagie 2001).

In the spring study, lizards from the coastal population (larger groups and larger population) were captured from a group consisting of 14 individuals, and those from the inland from groups of four or less. The fact that the inland population (smaller groups) thermoregulated less proficiently suggest that the observed population-level variation in thermoregulation may be related to varied levels of predation risk associated with variable group sizes, and that group-living confers thermoregulatory benefits to *C. cataphractus*.

Because the effective predation risk (experienced by animals) will vary proportionally to group-size (Krebs and Davies 1993), the response is expected to be present throughout the day, for example, members from smaller groups are expected to predominantly remain closer to their crevices. It may therefore be that lizards from the inland population remained close to crevices (due to increased equilibrium predation risk), experiencing lower T_bs than were potentially available to them during the early hours of the day, in principle avoiding thermally suitable microsites. Operative environmental temperatures are in general cooler near crevices in the habitat of *C. cataphractus* (Chapter 3). As the rocks heated up, the available T_es near crevices increased. This may explain why the mean T_b was higher than mean T_e from 15h00 into the night at the inland population. The fact that the effectiveness of

the thermoregulation index ($d_e - d_b$) was below zero from 9h00 to 10h00 at the coastal population suggest that lizards were not yet fully active and still experienced the cool T_es within crevices seeing that some *C. cataphractus* individuals may only become fully active at 10h00 (Visagie 2001).

(4) Thermal habitat quality

The fact that mean thermal habitat quality did not vary significantly among the inland and coastal populations in spring, suggests equal thermoregulatory opportunities/costs. Environmental operative temperatures (T_e) however did vary, being significantly lower at the inland population. The frequency distribution of T_es further indicates that the coastal population was provided with a wider range of thermal opportunities than the inland population suggesting that the varied accuracy and effectiveness of thermoregulation during spring was related to differences in local thermal environments.

The thermal exploitation index (E_x) assesses thermoregulation solely during periods when thermally suitable T_es (within T_p) are available within the habitat, therefore in theory enabling comparisons among species or populations inhabiting different thermal environments (Christian and Weavers 1996; Blouin-Demers and Nadeau 2005). Both the thermal exploitation and $d_e - d_b$ (effectiveness of thermoregulation) index indicated that lizards from the inland population were not fully exploiting the potential favourable T_es, suggesting that the deficient thermoregulation was not principally the result of the lower T_es. Additionally, although the thermal habitat quality of the inland population was higher than that of the coastal during the morning hours (7h00 – 12h00), accuracy of thermoregulation was lower during that time, further supporting the notion that the varied effectiveness and accuracy of thermoregulation was not the result of thermal factors.

(5) Unrealistic model placement

The T_e-models were similarly positioned around rocks among the localities and it therefore seems unlikely that inappropriate model placement was the cause of varied thermoregulation or negative $d_e - d_b$s. It is, however, known that thermal quality naturally varies dielly around rocks due to solar cycles (Huey *et al.* 1989; Kearney 2002) and it may

be that the sampled lizards inhabit unfavourable sections around rocks due to physical constraints (i.e. position of crevice relative to the four major wind directions (Chapter 3)).

   (6) Eurythermy

Alternatively, a degree of eurythermy may explain the observed variation in thermoregulation and negative $d_e - d_b$s at the inland population (i.e. act as thermal generalists). The fact that *C. cataphractus* has been shown to have a highly repressed resting metabolic rate and a degree of thermally independent metabolism (Mouton *et al.* 2000b), may suggest wide performance breadths and a degree of eurythermy. Individuals from both populations however moved from crevices and behaviourally thermoregulated in a laboratory photothermal gradient during both autumn and spring (Chapter 2). The presence of a definite T_p range and the fact that this range did not significantly vary among populations or across seasons (Chapter 2) suggests the absence of varied degrees of eurythermy among populations.

   The present interpretation is that that secondary influences are more likely constraining effective body temperature control. In particular, predation risk seems to be the most probable explanation for the observed geographic variation in the thermoregulatory activity and apparent avoidance of thermally suitable microsites by *C. cataphractus* during spring. This suggests that group-living may increase thermoregulatory capacity in *C. cataphractus*, by benefiting time budgets and promoting movement from crevices. The high number of unretrieved lizards during spring is unfortunate and weakens the strength of the argument. Field observations in both populations will complement the current results and lead to a more accurate interpretation. An alternative and more realistic approach to assess the effect of group-living on thermoregulation will be to compare thermoregulation among groups of varying sizes within a single population.

   In the meta-analysis of thermoregulatory investment in reptiles by Blouin-Demers and Nadeau (2005), the authors reiterated the need for studies performed on individuals when faced with different costs to better explore within-species cost-benefit balances. The current comparison of aspects of the thermal ecology of *C. cataphractus* among autumn and spring

represents such a scenario where populations are faced with varied thermoregulatory costs resulting from varied environmental temperatures among seasons.

The current results indicate that during spring, mean T_b deviated markedly from T_p at both populations, relating to low thermoregulatory accuracy (high d_b) in spite of the presence of favourable T_es (within T_p). In contrast, both populations accurately maintained T_b within T_p (i.e. high thermoregulatory accuracy, low d_b) during the dry autumn, when (food) energy constraints related to group-living is expected to climax (Mouton *et al.* 2000a), and therefore suggest that group-living and the associated low food availability and its effect on *C. cataphractus* (in terms of potentially lowered activity and altered energy budgets) does not reduce the thermoregulatory capacity of the species.

The index of effectiveness of thermoregulation ($d_e - d_b$) suggests that the accurate maintenance of T_b within T_p during autumn was achieved through behavioural thermoregulation in the coastal population. In the inland population, $d_e - d_b$ equalled zero for the majority of activity time suggesting that the accurate maintenance of T_b in T_p observed at the time occurred passively through thermoconformation in a highly favourable thermal habitat (since T_es within the preferred temperature range were abundantly available). In fact, the mean $d_e - d_b$ observed in the inland population of *C. cataphractus* corresponded closely to the value reported for *Anolis gundlachi* (0.5ºC) (Hertz *et al.* 1993; Blouin-Demers and Nadeau 2005), a lizard that Hertz *et al.* (1993) described as an archetypal (typical) nonregulator that rarely basks during activity.

Mean effectiveness of thermoregulation during day-time ($d_e - d_b$) (7h00 − 19h00) was significantly higher during spring (when thermal habitat quality was low) than autumn (when thermal habitat quality was high). This result corresponds to the general trend for thermoregulatory investment of reptiles observed in the meta-study by Blouin-Demers and Nadeau (2005), suggesting increased investment when thermal habitat quality is low (Blouin-Demers and Nadeau 2005; Row and Blouin-Demers 2006; Edwards and Blouin-Demers 2007), and may suggest thermoregulatory behaviour in conflict with the cost-benefit model of thermoregulation (Huey and Slatkin 1976). The high thermoregulatory accuracy (i.e. low

deviation of T_b from T_p) observed in both populations during autumn however indicates successful thermoregulation, and suggests that the observed seasonal variation in $d_e - d_b$ was not related to cost-benefit considerations, but simply in response to varied thermoregulatory requirements posed at the respective seasons.

Moreover, the hourly pattern of $d_e - d_b$ in spring shows that the actual difference portrayed by the higher mean $d_e - d_b$ occurred predominantly after 15h00 in the inland and 16h00 in the coastal population. *Cordylus cataphractus* has the largest fat bodies in proportion to body mass reported among cordylids, principally deposited during spring (Flemming and Mouton 2002) when perennial flower blooms support high invertebrate abundance (Struck 1994). The importance of increased effectiveness of thermoregulation ($d_e - d_b$) (i.e. active thermoregulation) during the late afternoon period in spring may therefore aid digestive processes (Stevenson *et al.* 1985; Van Damme *et al.* 1991).

The $d_e - d_b$s reported for reptiles range between $-0.3\ ^oC$ and $8.4\ ^oC$ (Blouin-Demers and Nadeau 2005; Row and Blouin-Demers 2006; Edwards and Blouin-Demers 2007). The overall mean $d_e - d_b$ of *C. cataphractus* (based on the current results across seasons and among populations) was $1.74\ ^oC$, and the species can therefore (relative to values known for other reptiles) be classified as a relatively poor thermoregulator.

The thermal exploitation index (E_x) (Christian *et al.* 1996) indicated that lizards exploited the favourable thermal opportunities more effectively during autumn than spring. The seasonal trend in E_x therefore suggests thermoregulation in accordance with the cost-benefit model of thermoregulation (Huey and Slatkin 1976), particularly indicating increased thermoregulatory investment during the more thermally favourable autumn in both populations (Huey and Slatkin 1976). The current E_x data were based on T_b and T_e measurements taken from between 10h00 and 18h00 which represents most of the typical daily activity time of the species (Visagie 2001), and the hourly pattern of E_x clearly indicates that lizards were exploiting the available thermally favourable opportunities more proficiently during autumn than spring. The discrepancy between the $d_e - d_b$ and E_x results may be related to the nature of each index, since these indices describe different aspects of

thermoregulatory investment (Blouin-Demers and Nadeau 2005). If *C. cataphractus* indeed remains within crevices for the vast majority of time during autumn as has been reported by Visagie (2001), the high E_x indicates that individuals were effectively exploiting the thermally favourable microclimates available to them during autumn, even though they were confined to crevices.

The correlation function of thermal habitat quality (d_e) versus thermoregulatory accuracy (d_b) had a slope (m) < 1 in both populations during autumn, suggesting an increase in thermoregulatory investment functional to decreased thermal habitat quality (Edwards and Blouin-Demers 2007), therefore contradicting the prediction of the cost-benefit model of thermoregulation (Huey and Slatkin 1976). During spring, the correlation between d_e and d_b of the inland population showed a slope of nearly one (m = 1) suggesting that lizards tended towards thermoconformation, whereas the coastal population had a slope exceeding one (m > 1) suggesting increased thermoregulatory investment as a function of increased thermal habitat quality, as predicted by the cost-benefit model (Huey and Slatkin 1976).

Chapter 3 of this thesis provides a more detailed description of micro-scale variation in thermal habitat quality at the coastal population during autumn, and indicates that crevices and crevice-edges were thermally more favourable than microsites outside of crevices during midday (11h00 – 15h00). Since *C. cataphractus* is known to remain within crevices for extended periods at the time, and thermal habitat quality deteriorates outside of crevices during midday, the more favourable T_es experienced by lizards (within crevices) portray an increase in thermoregulatory investment, but in reality, is simply the result of increased thermal habitat quality within crevices relative to that in the open.

Staged laboratory trials where the effectiveness of thermoregulation is monitored in relation to varied operative environmental temperatures and other costs such as predation pressure, social interactions and resource limitations will be useful in further describing the validity of the cost-benefit model of thermoregulation for *C. cataphractus* (Herczeg *et al.* 2006; Herczeg *et al.* 2008). The current results highlight the importance of using multiple thermoregulatory indices in concert and, further, to consider these indices as a function of

the time of day since simple daily means would have lead to totally different interpretations regarding the thermal ecology of *C. cataphractus.*

4.6 Conclusion

In spring, lizards in the more dense coastal population thermoregulated with higher accuracy than those in the less dense inland population. In addition, the index describing the effectiveness of thermoregulation performed ($d_e - d_b$) showed a large proportion of negative values (indicating avoidance of thermally suitable microsites) at the inland population in spring, coinciding with the generally inaccurate maintenance of T_b within T_p observed at the time. Predation risk is known to decrease proportionally to increased group-size and is also a notable source of avoidance behaviour in reptiles (Hayward 2008). The difference in thermoregulation among localities and avoidance of thermally suitable microsites at the inland population was most likely due to differential predation risk related to the different group-sizes. The current study therefore provides anecdotal evidence suggesting group-living increases thermoregulatory capacity due to the reduction in predation risk associated with such a life strategy. Collectively the accuracy of thermoregulation and thermal exploitation indices suggest that thermoregulatory success and investment occurred in accordance with the cost-benefit model of thermoregulation at seasonal scale, in particular, being higher during autumn when the thermal habitat was more favourable. Moreover, the fact that both the inland and coastal populations of *C. cataphractus* thermoregulated accurately during the annual peak in food scarcity (autumn), suggests that the amplified food constraints during the dry season associated with permanent group-living (Mouton *et al.* 2000b) do not compromise themoregulation in the species.

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