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RETREAT-SITE SELECTION IN THE COMMON FLAT LIZARD
(Platysaurus intermedius)

Lorraine Egan

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 1997.

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university, nor has it been prepared under aegis or with the assistance of any other body or organisation or person outside the University of the Witwatersrand, Johannesburg.



(Lorraine Egan)

9th day of November, 1998.

ABSTRACT

Numerous studies have shown that reptiles are able to assess their environment and select retreat sites based upon this assessment. Two main reasons proposed to explain retreat choice are predator avoidance and thermoregulation. In my study, I conducted laboratory experiments on 16 *Platysaurus intermedius* in an attempt to elucidate what cues are used in retreat site selection in these lizards. *Platysaurus intermedius* use rock crevices as retreats and I tested whether crevice height, depth and the thickness of the roof were important cues. I also measured selected body temperature in a thermal gradient. Field measurements of lizard body temperature as well as crevice temperature of retreats not used by the lizards were recorded and compared. *Platysaurus intermedius* show a significant preference for narrow and deep retreats. This would appear to reflect an efficient anti-predatory tactic with minor potential thermoregulatory consequences. Potential predators observed in the field would be unable to gain access to these lizards during the period that they are sequestered. No significant differences in retreat or temperature selection (in the laboratory experiments) by different age groups or different sexes were observed. However, temperatures selected in the laboratory were considerably higher than those available in the field. This observation possibly reflects an environmentally imposed limitation to thermoregulation to lizards in the field. Field recordings of lizard body temperature (when inside retreats) and the temperature of retreats not used by *P. intermedius* revealed that occupied crevices had significantly higher temperatures than unoccupied crevices. This indicates that *P. intermedius* may use temperature as an environmental cue by which to select a suitable retreat. It would thus appear that predation risks as well as thermoregulation are considerations for *P. intermedius* when selecting a retreat site, however it is difficult to say with any confidence whether predator avoidance or thermoregulation is of more importance.

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This dissertation is dedicated to my mother

MARGARET EGAN

Thanks for everything!

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LIST OF ABBREVIATIONS

SVL - snout-vent length

Te - environmental temperature

Tb - body temperature

°C - degrees Celsius

g - gram

mm - millimetre

cm - centimetre

hr - hour

p - the probability obtained in the course of applying a test of statistical significance.

SD - standard deviation

n - sample size

$F_{(d.f.)}$ - the ratio of two independent error mean squares (F statistic), degrees of freedom subscribed.

CHAPTER 1

INTRODUCTION

Despite the wealth of southern African reptiles, their ecology and physiology have received little scientific attention, with existing research being primarily of a descriptive and/or taxonomic nature. Habitat and microhabitat selection, in particular, has remained largely unexplored. These are undoubtedly important components of an animal's ecology, influencing the animal's survival both from an antipredatory and thermoregulatory point of view. My study aims to investigate the dynamics of retreat-site selection in the common flat lizard, *Platysaurus intermedius*, in an attempt to elucidate what factors influence retreat-site selection in these lizards and what impact the choice of a particular retreat has on it's ecology and physiology.

1.1 RETREAT UTILISATION

The utilisation of retreats by diurnal as well as nocturnal ectotherms has been well documented. Disused animal burrows are used as retreats by, amongst others, *Varanus gouldii* (King, 1980), *Varanus salvator* (Traeholt, 1995) and *Varanus bengalensis* (Wikramanayake and Dryden, 1993), *Chemidophorus* species (Schall, 1977) and *Ctenosaura similis* (Burger and Gochveld, 1991). Holes in tree trunks (e.g. *Varanus varius*, Stebbins and Barwick, 1968), hollows between the tree trunk and the bark (e.g. numerous nocturnal geckos, Bustard, 1967; Dial, 1978) and rock crevices (e.g. *Thamnophis elegans*, Huey, Peterson, Arnold and Porter, 1989 and *Platysaurus intermedius* and *Mabuya* sp., pers. obs.) are examples of other retreats utilised extensively by reptiles. However, studies of retreat-site selection, where researchers have shown that reptiles choose particular sites from a suite of available sites, are uncommon. Such studies require a sufficient sample of nests or

retreats for statistical analysis to be located, and this is often difficult (Burger and Gochveld, 1991).

The idea that animals "select" particular habitats is dependent on the assumption that they are able to assess what is available. Structural environmental features can often be used to successfully describe habitat and to distinguish habitats of different species. However, the question still remains as to whether or not the animals are using these structural features as cues during habitat selection (Reinert, 1993).

Numerous studies have shown that animals do posses the ability to assess their habitat. Brown and Brooks (1994) found that individual snapping turtles (*Chelydra serpentina*) were able to locate and recognise hibernation sites with characteristics facilitating overwinter survival. These characteristics may include adequate levels of atmospheric or aquatic oxygen, shelter or concealment from predators and protection from subzero temperatures. Although they could not recognise the exact characteristics upon which site choice was based, it was clear that site choice was not random. Martin, Lopez and Salvador (1991) found that the amphisbaenian *Blanus cinereus* avoids soils with high clay content, preferring sandy soils which are easier to dig in. Vegetation also had an indirect effect on microhabitat selection. Trees and bushes provide leaf litter on the ground around them and a layer of humus that favours invertebrates. They also provide shade that could be useful to *B. cinereus* in the hottest hours of the day (Martin et al., 1991). Robertson and Weatherhead (1992), by experimental manipulation of water temperature relative to air temperature, revealed that temperature influenced microhabitat selection by northern water snakes (*Nerodia sipedon*). According to Jackson (1988), a crucial attribute of an acceptable crevice for musk turtles (*Sternotherus*) is that the turtle is able to touch it's carapace to the ceiling. He suggested the possible use of darkness of a retreat as a cue by which the turtles judge crevice height. Schlesinger and Shine (1994) noted that the restriction of velvet geckos (*Oedura lesueurii*) to certain rock crevices, in itself, suggests that they have specialised requirements for nocturnal retreats. Their study demonstrated that these geckos are selective and indeed evaluate certain structural as well as climatic characteristics of their habitat.

Another behaviour where definite habitat selection occurs based on assessment of the habitat is an animal's choice of a suitable nest site. Nest site selection is an important aspect of the breeding biology of vertebrates because it directly affects fitness (Bull, 1987). Not only does nest placement affect predation rates in reptiles, but also affects incubation temperature that can determine sex ratios (as Bull, 1987, noted in the case of the Australian lizard *Trachydosaurus rugosus*), mortality and subsequent behaviour of hatchlings (Burger, 1993).

As with retreat site selection, numerous studies have been performed. In a study on nest site selection in lava lizards (*Tropidurus* spp.) in the Galapagos Islands, Burger (1993) found that in most colonies, the lizards' choice of nest site differed significantly from the available cover within the colony. Plummer (1990) monitored the behaviour of nine gravid green snakes (*Opheodrys aestivus*) implanted with radiotransmittors. All snakes observed exhibited directional nesting movements, suggesting a remarkable ability for remote detection of suitable nesting sites. Some nest chambers (tree hollows) did contain eggshells from previous years and it is more likely that the snakes returned to sites previously used (Plummer, 1990).

Two main reasons for the selection of retreat sites by ectotherms that have been addressed in the literature are predator avoidance and thermal considerations, which have also been suggested to reflect evolutionary constraints (Burger and Gochveld, 1991).

1.2 RETREAT SELECTION AND PREDATOR AVOIDANCE

Predation has long been implicated in the evolution of several morphological and behavioural characteristics of animals (Lima and Dill, 1989). Growing evidence also suggests that animals have the ability to assess and behaviourally influence their risk of being preyed upon. This involves trade-offs between the risk of predation and the benefits to be gained by engaging in a particular activity that may increase predation risk. Since an animal

must accomplish more in its lifetime than simply avoiding predation, its antipredatory adaptations should somehow be sensitive to current levels of predation risk. Such antipredatory flexibility may be achieved by integrating gross morphological adaptations with the behavioural decision-making process. Because the Tb of ectotherms is labile and greatly affected by environmental temperature, one would expect the economics of predator avoidance to differ from that of endotherms (Weatherhead and Robertson, 1992).

It has been recognised that predators can determine the extent of habitat use of their potential prey, an important aspect of this phenomenon being that habitat features influence predator efficiency (Mbahinzireki, Uiblein, and Winkler, 1991). To show that habitat selection by an animal is influenced by the presence of predators, it is necessary to demonstrate that there are predators which hunt for it and that the success of the predator is a function of the microhabitat that the prey has selected (Mbahinzireki et al., 1991).

It is logical that nocturnal retreats, whatever thermal conditions they offer, should also offer protection against predation. Protection from predators may in fact be of overriding importance in retreat site selection with thermal considerations being a secondary consideration. Sleep-sites should be selected to provide the animal with maximum security during its immobile state and, if a sleep site proves to be of good quality, an animal should continue to use that site (Clark and Gillingham, 1990). Sleep-site fidelity has been demonstrated in several cases e.g. lace monitors (Stebbins and Barwick, 1968) and Galapagos land iguanas (Christian, Tracy and Porter, 1984).

It may therefore be important for a lizard to choose retreats to which predators cannot gain access. If this is the case, the animal would usually be selecting a retreat based on structure, and according to Clark and Gillingham (1990), visual cues may be used to locate sites. As has been noted in M'Closkey, Deslippe, Szpak, and Baia (1990), habitat structure is an important component of nest, oviposition and site choice in insects (Alcock, 1987), amphibians (Howard, 1978) and reptiles (Heatwole, 1977; Rauch, 1985; Burger and Zappalorti, 1986; Adolph, 1990 and Law and Bradley, 1990). Sexton (1959) found that

painted turtles (*Chrysemys picta*) concentrate in patches of vegetation with a "T" structure regardless of vegetation composition (Heatwole 1977).

In crevice dwelling species, the height of the opening is possibly an important determinant of retreat choice. Shine (1991) found that large blacksnakes were unable to enter narrow crevices to obtain prey items. The crevice limitation hypothesis, however, assumes that small prey tend to be found in smaller crevices and that available crevices are narrow enough to exclude predators. Field data on the validity of these assumptions are lacking and would be of value (Shine, 1991). Furthermore, it is possible that differential responses to predation are the cause of age class microhabitat differences (Paulissen, 1988).

1.2.1 FACTORS AFFECTING ANTIPREDATORY BEHAVIOUR

SEX/GENDER

The gender of an animal may have an influence on antipredatory behaviour. Differing vulnerability to predation by either sex may alter antipredatory behaviour and tactics. Gravid female *Uta stansburiana* are thought to be more vulnerable to predators because they are slower (due to the burden of carrying their clutch) and may also be more conspicuous due to increased basking frequency (Wilson, 1992). Sexual dimorphism (e.g. bright coloration or bigger size of either sex) may also result in one sex being more conspicuous, and hence more vulnerable, than the other.

1.3 TEMPERATURE AND RETREAT UTILISATION

1.3.1 THE IMPORTANCE OF TEMPERATURE TO ECTOTHERMS

Body temperature (Tb) profoundly affects the ecology of ectotherms by influencing both physiology and behaviour (Huey and Stevenson, 1979; Porter and Tracy, 1983 and Stevenson, Peterson, and Tsuji, 1985). Thermal optima have been demonstrated in reptiles for a variety of physiological functions, as well as for the behaviours that depend on them (Troyer, 1987). Furthermore, different temperature optima exist for different functions e.g. in garter snakes, Tb's in the 25-35 °C range appear to be best for escaping predators, growth and, often, foraging, but for some ecological situations, the normal activity range is unavailable e.g. when hunting aquatic prey, the snakes often forage in water as cold as 13 °C (Stevenson et al., 1985). O'Conner and Tracy (1992) suggest that toads may select different "optimal" body temperatures (e.g. optimal for locomotion or for water conservation) depending on their environment and/or physiological state. Furthermore, critical temperatures may differ with body size within a species e.g. Doughty (1994) found a significant relationship between the critical thermal minimum (CTMin) and body size in garter snakes (*Thamnophis*).

The physiological processes affected by Tb range from elementary enzyme reactions up to whole animal functions such as metabolism, growth, locomotion (Van Damme, Bauwens, Vanderstighelen, and Verheyen, 1990 and Bennet, 1980), hearing ability and recovery from injury (Stevenson et al., 1985). Behaviour is the result of complex and integrated physiological processes and behavioural capacities are strongly limited by metabolic support systems (Bennet, 1980). The thermal dependence of such functions may be especially critical for terrestrial reptiles and amphibians, many of which routinely experience changes in Tb of 15-30 °C during the course of a day (Stevenson et al., 1985).

Weatherhead and Robertson (1992) found a significant effect of water temperature on swimming speed of northern water snakes (*Nerodia sipedon*). They were able to swim faster in warmer water (i.e. when Tb is higher) than in colder. Low Tbs experienced by *Anolis gundlachi* at high elevation may dramatically reduce sprinting ability (Hertz, 1992). Temperature has been found to influence sprint rates of land iguanas (*Conolophus pallidus*) with maximal sprint rates occurring between 31.7 °C and 40 °C (Christian and Tracy, 1985). Sprint rates are relevant to adult land iguanas during territorial disputes, fights and frequent chases (Christian and Tracy, 1985). Burst locomotor performance in five species of anuran amphibians was found to be significantly affected by experimental temperature (Knowles and Weigl, 1990).

The relationship between temperature and performance may not be fixed but may shift with ontogenetic stage, with acclimation or physiological state, or among individuals. Moreover, different physiological functions sometimes vary in their thermal sensitivities (Huey, 1991).

Thermal constraints exist because the Tb of ectotherms is a complex function of its biophysical environment (Grant and Dunham, 1988). Thermoregulation can be defined as an active regulatory process involving behavioural and/or physiological adjustments to maintain Tb as close as possible to an independently defined "set point range". It can be demonstrated by showing that Tb of an animal differs significantly from those of a null model (Hertz, Huey and Stevenson, 1993). As ectotherms, reptiles depend primarily on external sources of heat for determination of their Tb. Some species actively maintain Tb within limits that are narrower than those possible in the given environment. Reptiles move between thermal sources and sinks, maintaining their Tb by thermal exchange with the environment, and have complex mechanisms for temperature perception as well as abilities to increase or decrease rates of heat exchange between the body and the environment (Gans and Dawson, 1976).

Heliotherms, such as lizards, that bask, constantly monitor the position of the sun and amount of available heat and make behavioural adjustments to maintain their Tb at some "selected" temperature (Sievert and Hutchison, 1989). It is thus obvious that the control of

Tb in reptiles is largely dependent on appropriate exploitation of their thermal environment as well as the availability of required thermal conditions in the environment (DeWitt, 1967). The geographic distribution of ectotherms is limited in part by their dependence on sources of environmental heat to maintain Tb (Doughty, 1994).

The habitat occupied by an animal, by determining microclimates that the animal experiences, influences the animal's physiological capabilities and ultimately its ecological performance. With respect to ectotherms, temperature is a key environmental variable, one that is physiologically significant as well as easily measured and manipulated (Huey, 1991). Because digestive rate, speed of locomotion, foraging efficiency and reproductive success are all related to Tb, thermal conditions are often regarded as one of the most important proximate factors in habitat selection. However, several studies have demonstrated that some reptiles expend little effort in precise thermoregulation (Reinert, 1993). Therefore, the importance of thermoregulatory behaviour and thermal preference in habitat selection should not simply be assumed without careful evaluation e.g. habitats with optimal thermal regimes and suitable shelters are useless without an adequate food supply (Reinert, 1993) or it may be too costly for the animals to thermoregulate (Huey and Slatkin, 1976). Habitat use by a particular species reflects an overlap between microhabitats that are thermally suitable and those that are suited to its morphology and behavioural preference (Adolph, 1990). It has been postulated that exploitation of some habitats and avoidance of others allows many lizards to maintain Tbs within a range allowing for maximal performance of ecologically relevant functions (Waldschmidt and Tracy, 1983 and Huey et al., 1989). Careful thermoregulation also reduces the possibility that ectotherms will be exposed to extreme, potentially lethal Tbs (Huey et al., 1989). An optimal strategy for habitat selection should involve response to indicators of primary limiting variables (Law and Bradley, 1990). Heatwole (1977) predicts that an optimal strategy in habitat selection would be response to several simple but constant factors that are good habitat indicators. Microhabitat selection in ectotherms may be related to microclimate or to preferred thermal conditions and such a choice may have a direct bearing on individual fitness (Law and Bradley, 1990).

Selection of favourable microhabitats and their associated micro-climates is a form of behavioural thermoregulation (the operational definition of behavioural thermoregulation being: "non-random orientation towards environmental factors that influence Tb" (Adolph, 1990) and according to Bartholomew (1982, in Diaz, 1991) and Harwood (1979), behaviour is the principle agent of temperature regulation in reptiles with the role of physiological control being, at best, one of potential modulation. Very small reptiles (< 20g body mass), in particular, are generally not accepted to have significant physiological control over their rates of heating and cooling (Turner, 1987). According to Crisp et al., 1979 (in Diaz, 1991), in small and medium-sized diurnal baskers, Tb changes so rapidly that physiological control is negligible in comparison with behavioural adjustments. Because the potential for behavioural thermoregulation in reptiles depends on the availability of suitable microclimates, the thermal structure of the environment should influence patterns of activity and habitat use (Weatherhead and Robertson, 1992).

A number of studies have demonstrated selection of microhabitats in ectotherms based on temperature e.g. garter snakes (Huey et al., 1989). It has been well documented that reptiles make use of diverse habitats during the day to reach and maintain their thermal preference e.g. *Lacerta sp.* (House, Taylor and Spellerberg, 1980) and *Chrysemus picta* (Schwarzkopf and Brooks, 1985). Castilla and Bauwens (1991) noted that in *Podarcis hispanica atrata*, the most conspicuous thermoregulatory behaviours were to adopt basking postures and shuttling between sun and shade. The animals were thus able to confine Tb to a narrow range largely independent of air or substrate temperature and showing little diel fluctuation (all features commonly linked to a high degree of thermoregulatory precision). Spotted tree monitors (*Varanus scalaris*) were found to exploit thermal refugia allowing them to maintain Tbs within their set point range for much of the day (Christian and Bedford, 1996). An added benefit of being concealed in refugia (posts and tree hollows) is no exposure to predators, thus constituting a behaviour that can be termed cryptic thermoregulation (Christian and Bedford, 1996).

Behavioural mechanisms of thermoregulation have received much less attention than their ecological consequences. Environmental cues (characteristics of the physical environment that determine the choice of a particular strategy) and ecological implications (association with other relevant traits such as time allocated to foraging or predator escape) of these behavioural alternatives remain largely unexplored (Diaz, 1991). It is generally assumed that behavioural and physiological mechanisms of thermoregulation are adaptive since thermoregulating lizards are likely to avoid dangerously extreme Tb and achieve some control over metabolic processes (Huey and Slatkin, 1976). My study examines the possibility that retreat selection in *P. intermedius* is primarily a behavioural thermoregulatory tactic and explores the thermoregulatory consequences of selecting particular retreat sites.

1.3.2 PROBLEMS WITH PREVIOUS STUDIES ON THERMOREGULATION

Most studies on thermoregulation have considered only periods of activity and in field work there has usually been an attempt to exclude Tbs of lizards before they have become active (Ruibal and Philobosian, 1970; Ruben, 1976). However, times of activity are short in most reptiles, especially in herbivorous and temperate zone species (Huey, 1982), many of which spend the greatest part of the day sequestered in retreats (Huey et al., 1989). An example of this is provided by Grant (1990) who found that in summer, *Sceloporus merriami* were inactive and retreated to deep crevices and caves during mid-afternoon. Furthermore, not all individuals in some temperate zone species are active daily, even when weather conditions permit (Huey, 1982).

Apart from the obvious benefits of activity (e.g. increased access to food, opportunities for temperature regulation, access to potential mates and opportunities to monitor and defend territories), there are also important disadvantages (e.g. increases risk of predation, risk of injury in territorial encounters and the expenditure of energy and water) (Huey, 1982). The

cost of activity required to capture prey by a reptile may outweigh the benefits derived from feeding and inactivity may then be favoured (Gans and Pough, 1982).

Therefore, the apparent careful thermoregulation of active, exposed ectotherms may present an incomplete and potentially misleading portrait of their thermal biology over the entire 24-hr period. Depending on the thermal properties of their retreat sites, sequestered ectotherms may have different opportunities for thermoregulation and may thus experience Tb very different from those associated with aboveground activity. Consequently, the retreat sites selected by ectotherms may have a profound impact on energy budget and growth (Huey et al., 1989).

It is easy to assume that inactive reptiles have relinquished control over their thermal fate and are thermally passive. However, reptiles have two ways of thermoregulating during inactivity. Selection of retreats controls microclimates experienced during inactivity e.g. some reptiles select retreats in burrows, leaf litter or boulders to gain access to warm and stable thermal microenvironments (Heatwole, 1970, Porter, Mitchell, Beckman and DeWitt, 1973). Reptiles can also regulate Tb by changes in position within these retreats (Huey, 1982). Schlesinger and Shine (1994) suggested that velvet geckos (*O. leuesurii*) actively thermoregulate within diurnal shelters by means of indirect basking (contact with sun-warmed surfaces within the shelter).

Thus it may be a misconception that reptiles are always cold or thermally passive while in their retreats. Some reptiles may be able to control body temperature more precisely while in retreats than when above ground. Even reptiles that remain stationary at a depth of 20 cm can achieve suitable body temperatures for about 14 hr per day. Indeed, during the summer, *Dipsosaurus dorsalis* may be able to maintain its selected temperature for 24 hr a day without leaving it's burrow. Gravid *Cnemidophorus* are very secretive, but nevertheless thermoregulate carefully in the safety of their burrows (Huey, 1982). Of course, such precision is impossible in some retreats and in cooler seasons.

A number of studies have shown that thermoregulation within retreats is possible due to the diverse thermal structure offered by these retreats (e.g. Bustard, 1967; Humphreys, 1978; Schall, 1977; Andrews and Kenney, 1990 and Dial, 1978). It has been demonstrated that deeper burrows generally have higher temperatures than shallow ones during cooler parts of the day with the reverse being true during the hotter parts of the day for burrows of *Amphibolurus inermis*, this probably resulting in more stable temperatures in the deeper burrows (Heatwole, 1970). Both temperature and humidity of burrows become more stable with increasing depth (King, 1980). By entering burrows/retreats while retreat temperatures are still increasing relative to ambient temperatures, a reptile can increase the time spent at elevated Tb as is the case in the *Varanus gouldii* (King, 1980).

Nocturnal heat loss is also reduced in reptiles utilising retreats e.g. members of the genus *Thamnophis* utilise holes, crevices and leaf litter as retreats and are able to consistently maintain higher nocturnal Tbs than those unable to utilise these retreats (Ruben, 1976). Wikramanayake and Dryden (1993) suggest that the similarity between early morning and midday Tb of *V. salvator* and its use of microhabitats with relatively constant temperatures reflect the use of thermally stable microhabitats during the day and the night. *V komodoensis* and *V. giganteus* also use thermally stable, warm nocturnal microhabitats to maintain high Tb (Auffenberg, 1981 and King et al., 1989).Traeholt (1995) cites the use of burrows as sleep sites in water monitors (*Varanus S. salvator*) as being an important component of their thermoregulatory behaviour as it is an effective way to retain body heat (heat loss through radiation, convection and conduction is reduced). The impact of preferred sleep sites should be evaluated, as they must be important in maintaining relatively stable Tbs throughout the day/night cycle (Traeholt, 1995).

Despite the above considerations, thermoregulatory and physiological considerations of retreat site selection have rarely been studied (Huey et al., 1989) and little time has been devoted to analysing the microclimate available to or chosen by lizards during periods of inactivity (Christian et al., 1984). Retreat-site selection may have a profound impact on an ectotherm's thermal physiology and ecology (Huey, 1991).

Huey et al. (1989) demonstrated the importance of understanding the relationship between retreat site selection and physiological performance in garter snakes (*Thamnophis elegans*). These snakes spend long periods (sometimes several consecutive days, even in good weather) in retreats. Retreats usually comprised cavities under rocks, those available varying from small rock flakes to huge boulders. The magnitude of daily thermal cycles beneath the rocks was found to be strongly influenced by rock thickness. Thermal cycles were most variable under thin rocks where Te exceeded the critical thermal maximum of the snakes during the day and dropped to near the critical minimum of the snakes at night. Thermal cycles were least variable under thick rocks but available Tes were low and never reached the preferred range of the snakes. Thermal cycles were moderately variable under medium-thickness rocks (20-40 cm) and available temperatures were often within the preferred range.

The results obtained by Huey et al. (1989) suggest that thermoregulatory opportunities in retreats are often equivalent and sometimes superior to those available in the open and that the snakes appear to take advantage of those opportunities. The snakes tended to utilise rocks 20-40 cm in diameter and conspicuously avoided small rocks, which were abundant but got very hot during the day. Snakes selected intermediate-thickness rocks allowing them to spend a longer amount of time in their preferred Tb range. It has been suggested that because these snakes spend far more time in retreats than in above ground activity, physiological consequences associated with various retreat sites may be key factors in overall habitat selection by snakes (Huey et al., 1989).

1.3.3 WHY ECTOTHERMS MAY SELECT HIGHER NOCTURNAL BODY TEMPERATURES

As is evident from the previous review, very little time has been devoted to the study of nocturnal retreat selection. As my study focuses on nocturnal retreat-site selection, it is

important to consider why an ectotherm may want to maintain a higher nocturnal Tb. There are various possible reasons, the most important are the following:

DIGESTION

One external factor with a pronounced influence on the digestive processes in poikilothermic animals is the ambient temperature (Skoczylas, 1970). The digestive performance of many reptiles increases with Tb up to or even beyond the species preferred Tb, with an identifiable optimum temperature or temperature range (Troyer, 1987). Higher Tb in reptiles may enhance digestive performance by increasing the rate of digestion (van Marken Lichtenberg, 1992) as Troyer (1987) observed in *Iguana iguana*, or by other means such as increasing the secretion or activity of digestive enzymes or increasing the rate of microbial fermentation (Troyer, 1987). There is evidence to suggest that enzyme-substrate affinity in some European lizards and snakes is greatest at or near the species thermal preferendum (Harwood, 1979). In snapping turtles (*Chelydra serpentina*), both rate and efficiency of digestion are correlated positively with Tb (Knight, Layfield and Brooks, 1990). Digestive efficiency does not appear to be temperature dependent in all species and the pattern of association between temperature and digestive processes requires more extensive investigation (Troyer, 1987).

Many reptiles require and seek exposure to some source of external heat in order to digest their food properly even if they are not thermophillic at other times (Regal, 1966 in Troyer, 1987). According to O'Conner and Tracy (1992), toads (*Bufo woodhousei*) selected significantly lower Tb in a thermal gradient after being deprived of food for 48 hours. They concluded that this behaviour decreased metabolic demands. An increased Tb may increase digestive rate so as to prevent putrefaction of ingested food (Cowles and Bogert, 1944). A further advantage of faster digestive rate would be a decreased processing time (Harwood, 1979) allowing an animal to select higher Tbs for digestion during the season when prey/food is plentiful, increase their digestive rate, and thus potentially maximise rates of

energy accumulation for growth and reproduction assuming that increased metabolic costs did not negate the advantages of a faster processing time (Greenwald and Kanter, 197›).

Again, no universal principles can be applied to reptiles with regard to the relationship between temperature and digestion. In hatchling snapping turtles (*Chelydra serpentina*), the optimal Tb for digestion is high relative to the range of temperatures occupied by the turtles and one might expect satiated turtles to maintain higher Tbs than hungry ones (Knight et al., 1990). However, they did not exhibit a thermophilic response to feeding and Knight et al. (1990) suggested that nutritional status here affects selected Tb only because satiated animals tend to be more sedentary in the thermal gradient

MORNING EMERGENCE

Activity cycles of reptiles are strictly governed by the range of available temperatures within the habitat (Bustard, 1967). Tb upon emergence from the overnight period of inactivity may be important and it may be necessary for the animal to sleep in places where they come to some optimal "starting up" temperature in the morning (Christian et al., 1984). This may allow them to initiate activity earlier as they would require a shorter time to heat up in the morning. In *V. s. salvator*, how well the lizard can maintain Tb during the night is apparently important in controlling Tb near activity levels (Traeholt, 1995). An optimal starting up temperature may also have implications for predator avoidance in the early morning. The thermal environment can influence the vulnerability of ectothermic vertebrates to predation (Porter et al., 1973 and Christian and Tracy, 1981). The ability to escape predation is undoubtedly a function of Tb (Huey and Slatkin, 1976).

A number of studies have demonstrated that reptiles are more vulnerable and hunting success of their predators is greater at cooler times of the day and during the heating phase (e.g. Stevenson et al., 1985, with respect to garter snakes and their natural predator, hawks and Fox, 1978 with respect to hatchling Galapagos land iguanas and hawks). Tb influences

the defensive reactions and sprint speeds of some agamid lizards in the laboratory (Hertz, Huey and Nevo, 1982). The relative advantage of flight may be influenced by a change in physiological state, which could alter the probability that an animal may outrun a potential predator. The agamids studied by Hertz et al. (1982) have a powerful bite and this, coupled with a general scarcity of refugia probably explains why at Tbs that reduce sprint speed, they rarely run but instead become aggressive. Flight initiation distance in *Anolis lineatopus* is inversely correlated with body temperature, which constrains running ability (Rand, 1964). According to Schieffelin and DeQueroz (1991), antipredatory behaviour in garter snakes (*Thamnophis sirtalis*) is strongly affected by temperature, with the snakes being more active and aggressive at higher temperatures. They suggest a possible adaptive shift towards static defence when impaired locomotion at low temperatures makes flight an ineffective strategy. It was observed that at 10 °C, snake movement had slowed to such an extent that aggressive strikes were not an effective defence, at least against endothermic predators whose movement is not comparably retarded (Schieffelin and DeQueroz, 1991).

Apart from influencing locomotor performance, temperature also affects perceptive functions (Van Damme et al., 1990). Squamate reptiles have a well-developed ability to chemically recognise prey. Teiid lizards appear to use chemical cues in predatory behaviour e.g. tegu lizards (*Tupinambus teguixin*) are capable of detecting chemical food stimuli (Yanosky, Iriart and Mercolli, 1993). Tongue flicking (a means of chemically sampling the environment) could be adaptive in allowing assessment of the presence and quality of food, predators, conspecifics and possibly noxious chemicals (Cooper, 1994).

A variety of vertebrate prey react to scent products of snakes and certain prey use chemoreception to discriminate snakes that are harmless and those that are predators. The chemical discrimination of snake predators from snake prey by naive white-throated savannah monitor lizards (*Varanus albigularis*) has been demonstrated (Phillips and Alberts, 1992). Van Damme et al. (1990) conducted a study of the thermal dependence of chemoreceptive and behavioural responses towards snake (*Vipera berus*) chemical cues in the cool temperate lizard, *Lacerta vivipera*. Their finding that lizard tongue flick rates were

temperature dependent lead the authors to speculate that at a higher Tb, lizards should be able to explore an area more adequately and to perceive more quickly that no predator risk is nearby. This would allow them to resume other behaviours (e.g. foraging) more rapidly (Van Damme et al., 1990).

A contrasting view is that of Heath (1962) who has stated that many ectotherms use underground nocturnal retreats and may not be expected to begin daily activity until sufficient heat has penetrated into these shelters to warm them. Such a delay in emergence would result in the loss of valuable activity time on the surface during the morning. As an alternative, ectothermic animals could remain on the surface exposed throughout the night, but in the resulting cold comatose conditioned they would be subject to predation and possibly freezing. Incident solar radiation is the most important source of heat for an ectothermic animal during the early morning and the time spent with Tb below the voluntary mean would seem to be a compromise between the need to become active as early as possible and the risk of being exposed to predators for too long a period of time (House et al., 1980).

Heath's (1962) data on *Phrynosoma* appear to show that the initiation of activity in the morning is independent of temperature, at least when the animal is warm enough to move. The possibility of a circadian rhythm integrated with temperature regulation in reptiles is of considerable significance with regard to their biology as it offers a mechanism whereby an animal can secure a safe nocturnal shelter without losing activity time in the morning (Heath, 1962). However, variation in time of emergence of individual *Varanus gouldii* from their burrows on successive days suggests that environmental conditions rather than a biological rhythm determines the actual emergence time of this lizard (King, 1980). Thus, no universal principles with regard to morning emergence appear to apply to reptiles as a whole.

Associated with Heath's (1962) view is the idea that burrow and retreat entrances may be orientated to allow heating in the early morning at the entrance: orientation of the retreat entrance relative to the position of the sun is suggested to be important in the location of

burrows of the desert dragon (*Amphibolorus inermis*) (Heatwole, 1970) and black iguanas (Burger and Gochveld, 1991). The location of retreat entrances may be an important factor determining the period of aboveground activity in *P. intermedius* as they only emerge once the entrance is in full sunlight (pers. obs.).

Also, it may be unfavourable for some reptiles to maintain high nocturnal Tbs and orientation to high temperatures is not constant in reptiles (Regal, 1967). The tendency to orient voluntarily to low temperatures has been demonstrated in many lizards under conditions that would permit the animals to maintain Tbs constantly at activity levels (Andrews and Kenney, 1990; Regal, 1967 and Huey, 1982). This would be of benefit to the animal as a water and energy conservation mechanism (Regal, 1967 and Rismiller and Heldmaier, 1982). Under certain conditions, voluntary nocturnal hypothermia may prolong the potential foraging time the following day (Huey, 1982) e.g. on a hot morning, a *Gopherus* that initiates activity at a low Tb might presumably forage longer before overheating than can one initiating activity at high initial Tb (McGinnis and Voigt, 1971 in Huey, 1982). However, Marlow (1979 in Huey, 1982) found that tortoises spending the night in a state of hypothermia often have shorter foraging times, apparently spending a longer period basking before being able to commence foraging. Voluntary hypothermia and periodic inactivity may be essential for health, at least of captive reptiles as long exposure to constant high temperature can be stressful and periodic relief may be necessary (Huey, 1982). The voluntary orientation to low temperatures has survival value: at sunset, different parts of the habitat cool at different rates, so orientation to isolated warmer patches could lead the lizard away from shelter and perhaps make them more vulnerable to predation (Regal, 1967).

However, such considerations may be of minimal significance for small lizards due to their high surface area to volume ratios (Paulissen, 1988) relative to many of the other ectotherms studied with regard to thermoregulation e.g. iguanas and some larger snakes. Smaller reptiles would have much faster rates of heating and cooling (i.e. lower thermal inertia) (Paulissen, 1988) and would therefore be expected to heat up very rapidly in the morning

after emergence. Although Grant and Dunham (1988) have noted that thermal constraints are especially important for small lizards with low thermal inertia, for which a failure to select an appropriate microclimate for even a few minutes can result in temperature impairment or death, this may only apply in situations where temperatures approach critical minimums or maximums.

1.3.4 TEMPERATURE AS AN ECOLOGICAL RESOURCE

Grant and Dunham (1988) concluded that thermoregulating lizards are constrained to occupy specific thermal microclimates within their home ranges when they are active and, as has been discussed, similar principles may apply to periods of apparent inactivity. Because lizards are constrained by the thermal environment and thermally suitable sites may be limiting, competition for thermal microclimates may occur. Researchers have tended to consider the consequences of thermoregulation on competition and not the reverse (Huey and Slatkin, 1976). If we assume that animals compete for physical space in a particular habitat, then differentially distributed resources make some spaces more valuable than others (Waldschmidt and Tracy, 1983).

For more than a quarter of a century, ecologists have recognised that the thermal properties of habitats are important to resource partitioning by ectothermic vertebrates (Hertz, 1992). Magnuson, Crowder and Medvick (1979), in a theoretical discussion of environmental temperature as a partitionable (though not consumable) resource, proposed that "animals compete for and partition thermal resources " just as they partition space or food. Roughgarden, Porter and Heckel (1981), Tracy and Christian (1986) and Dunham, Grant and Overall (1989) subsequently clarified this assumption by identifying space and time as the dimensional units with which to quantify the thermal environment as a resource. Ecologists have rarely considered competition for thermal resources as it is difficult to envision the consumptive use of heat (Magnuson et al., 1979). However, occupancy of a particular microhabitat by an individual renders it unavailable to others although the resource

("T^{o}-space") is not used up. Competition can limit the spatial niche of a species and consequently limit the range of environmental temperatures available to the lizard (Ruibal and Philobosian, 1970). Tracy and Christian (1986) have stated that since space and time are clearly resources that can be exploited, they provide the units whereby the thermal environment can be quantified as a resource. If a resource is exploitable, then there can be competition for it (Tracy and Christian, 1986). While there can be no competition for any particular ambient temperature, the time or space in which an organism can attain optimal heat exchange can be objects of competition (Tracy and Christian, 1986). "T^{o}-space" may, theoretically, in some cases be just as important as other resources (e.g. food and mates) in defining territories. This necessitates that ectotherms have the ability to differentiate between environments with different thermal properties (already shown by the fact that selection based on temperature occurs) and that thermally favourable sites are limiting, even if only at certain times of the year. Only then can the activity of certain organisms (by social interactions) affect availability of "T^{o}-space" to others.

Web-building spiders (*Agelenopsis*) select habitats, in part, on the basis of thermal properties and that the spiders will fight for sites with optimal thermal qualities (Riechert, 1985). The thermal factors of a habitat, by determining activity times, have a major impact on the behaviour and ecology of these spiders (Huey, 1991). Some reptiles have been found to compete physically for limited thermoregulatory sites (Magnuson et al., 1979). For example, male *Klauberina riversiana* thermoregulate more carefully in the presence of another male and are able to prevent the latter from gaining access to a heat lamp (Regal, 1971 in Huey and Slatkin, 1976), *Sphenomorphus koskinskoi* prevent subordinates from gaining access to heat sources in the laboratory (Done and Heatwole, 1977) and large male *Anolis* seemingly exclude smaller males from habitats that may be thermally optimal (Rand in Huey, 1982).

1.3.5 COSTS AND BENEFITS OF THERMOREGULATION

Thermoregulation should be viewed as a cost benefit situation (Huey and Slatkin, 1976, Huey and Stevenson, 1979 and Carrascal, Lopez, Martin and Salvador, 1992) with one of the major costs involved being the risk of predation (Huey, 1982). Interactions with predators may force reptiles to abandon thermoregulation temporarily or reduce the precision of thermoregulation (Huey, 1982). Also, careful thermoregulation may assist in antipredatory tactics as factors like sprint speed (e.g. in *Lacerta monticola*, Carrascal et al., 1992) and aggression (e.g. in *Xantusia riversiana*, Mautz, Daniels and Bennet, 1992) are temperature dependent.

The costs and benefits of regulating a particular Tb within the available distribution of operative environmental temperatures derive from two principle sources (Grant, 1990). The first involves temperature dependence of physiological performance such as locomotor ability, food processing capacity and expenditure of assimilated energy and water resources on physiological maintenance and the second relates to how spatiotemporal variation in environmental temperature availability constrains activity and home range use. Gans and Dawson (1976) have stated that species apparently balance the costs involved in maintaining elevated temperatures against the benefits derived. Maintenance of an elevated temperature requires increased metabolic rate leading to an increased maintenance cost. A species may then decrease its daily, monthly or annual energy requirements by shifting to an elevated temperature only part of the time e.g. during digestion (Gans and Dawson, 1976).

One of the great advantages of ectothermy may be the flexibility it confers with the consequent ability to adjust selected Tb in response to the costs and benefits dictated by local environmental conditions. Many aspects of an organisms environment may interact to determine the relative magnitude of these costs and benefits (Shine and Lambeck, 1990). An example is provided by Crawford, Spotila and Standora (1983) who suggest that basking behaviour in *Chrysemys scripta* represents a compromise between the benefits of high body

temperature (e.g. increased digestive efficiency, increased energy for locomotion) and the costs of behavioural thermoregulation (e.g. reduced foraging time).

DeWitt (1967) suggests that allowing above normal Tb should benefit a lizard if it results in increased activity time. Therefore, the benefits of accepting a higher Tb and extending daily activity time for foraging and social interactions must be weighed against performance costs and resource expenditures resulting from higher Tb. A critical determinant of the trade-off is the increase in the fraction of usable habitat due to accepting microclimates where warmer Tbs can be obtained or alternatively, the decrease in the amount by which activity is constrained (Grant, 1990). Grant (1990) compared morning and evening distribution of available operative environmental temperature (Te) estimated by an array of randomly deployed and orientated copper models of desert lizards (*Sceloporus merriami*) placed on ground and rock surfaces within the lizard's home ranges. Available Te distribution in the evening forced lizards to accept higher activity Tb, therefore increased metabolic rate and water loss and lower locomotor performance or remain inactive in crevices and caves. Their data suggest that the distribution of available Te can directly influence the cost/benefit economics of lizard Tb selection.

From the previous discussion relating temperature and predator avoidance to retreat use, it is clear that thermal considerations and antipredatory tactics with respect to retreat-site selection are not necessarily mutually exclusive and selection may reflect a compromise between the two. Furthermore, thermoregulation and predator avoidance are not the only factors influencing microhabitat use/selection. One illustration if this is provided by Hertz (1992) who proposes several alternate hypotheses (apart from behavioural thermoregulation) to explain non-random choice of perches in some *Anolis* lizards: to gain access to prey that thermoregulate, to avoid predators that are more abundant or efficient in other microhabitats or to interact socially with other animals that are, non-randomly distributed.

1.4 OBJECTIVES OF STUDY

Although *P. intermedius* utilises retreats extensively during both the day and at night, my study addresses nocturnal retreat use only. The aims are firstly, characterising the physical and thermal properties of retreat sites used by *Platyscurus intermedius* and secondly, to establish whether retreat use is random or non-random. An attempt was made to ascertain whether retreat site selection, if it occurs, is related to thermoregulation, predation or a combination of both. To fulfil these aims, a number of specific questions were addressed:

1. Do the physical properties of retreats influence retreat utilisation by *P. intermedius*?

2. Can the utilisation of retreats be related to the thermal properties of those retreats?

3. Which retreat properties are most important in crevice choice?

4. What relationship, if any, exists between crevice utilisation and lizard sex and age?

CHAPTER 2

MATERIALS AND METHODS

2.1 STUDY ANIMAL

The Cordylid lizards of the genus *Platysaurus* are highly specialised for life on rock outcrops which weather to produce narrow fissures suitable as refuges (Broadley, 1978). As their name suggests, the body is extremely flattened enabling them to squeeze into narrow cracks. Up to 12 individuals may be found in the same crevice although it is unusual to find adult males together during the breeding season (Branch, 1988). They are restricted to suitable geological formations, principally granite, gneiss and sandstone (Broadley, 1978) and as a result, are found in isolated populations. They are sociable and form dense colonies with prime territories on rock surfaces being defended by dominant males during the breeding season (Branch, 1988).

Platysaurus lizards emerge from their retreats as soon as the sun warms up the rock face early in the morning. As the midday sun raises rock temperature to critical maximum, they will move into shade, returning to sunny spots later in the afternoon (Broadley, 1978). Emergence seems to be related to sunlight striking crevice openings (pers. obs.)

The body markings of members of the genus consist of two components: stripes and spots. Juveniles are dark brown to black with three light longitudinal stripes extending from the snout to the base of the tail. In some forms, there are light spots between the stripes (usually present on the flanks). Juvenile markings persist in adult females, but in males, the ground colour lightens and the stripes usually fade out on the body although often persisting on the head. At the same time, the spots become more pronounced (and vary in size and density)

Body markings of adult males are generally distinct from females and sub-adults due to their bright red tails and blue bodies, although considerable variation in the intensity of coloration occurs (Branch, 1988). The bright ventral colouration in males is used in male confrontation, as a deterrant to male conspecifics (Jacobsen, 1994) as well as during courtship as a sexual attractant (Branch, 1998).

Flat lizards appear to be sexually mature at the end of their second or third year. The first sign of approaching maturity in the male is the development of the femoral pores from the middle of the thighs outward, at the same time, a broadening of the head across the temporal region is usually noticeable. Testes are large and femoral pores are usually well developed before juvenile stripes begin to fade out and are replaced by the dorsal spots and the bright coloration of the mature male. A few sexually mature males retain juvenile coloration and markings but femoral pores are well developed. Genuine females with well developed femoral pores are rare (Broadley, 1978). Unlike other Cordylids, female *Platysaurus* are oviparous and lay two large, elongate eggs, usually in November-December. The eggs are soft-shelled and are laid in deep cracks, usually in damp leaf mould (Branch, 1988).

Most flat lizards feed on small invertebrates (flies, beetles and larvae) although some (including *P. i. wilhelmi*) also eat plant material (flower petals, young leaves and seeds). Predators of these lizards include snakes and other lizards (Branch, 1988).

The common flat lizard (*Platysaurus intermedius*) is the most widely distributed member of this genus, being found throughout most of Zimbabwe, the Northern Province ,and Mpumalanga, with peripheral races in southern Malawi, eastern Botswana, Swaziland and adjacent Mozambique and northern Kwa Zulu-Natal (Branch, 1998). Species and subspecies are often identified by the males' breeding colours, making identification of females and juveniles to species level difficult.

2.2 PRELIMINARY FIELD OBSERVATIONS

A preliminary field study on populations of *P. intermedius* at Pullen Farm, Mpu[illegible]nga (24° 35' S, 31° 11' E) was carried out in 1991. The physical and thermal properties of a number of retreat-sites were measured in an attempt to relate these properties to the utilisation of the retreats by *P. intermedius*. The number of lizards occupying each retreat was measured as the number of lizards emerging from each rock crevice in the morning during an observation period of two hours from the emergence of the first lizard. Observations were initiated before the rock outcrop received full sunlight and the lizards were not seen to emerge before this (pers. obs.). Retreat temperature was measured by inserting thermocouples into each crevice. Thermocouples were insulated with polystyrene and connected to an MS Systems 120 data logger which recorded temperatures at 15 minute intervals from 19h00 to 08h00. Rock thickness (the thickness of the rock forming the roof of each crevice), crevice height (the height of the entrance to the crevice) and crevice depth (measured by inserting a length of wire into the crevice) were recorded for each retreat.

Platysaurus intermedius were found to be clumped in distribution and utilised only a subset of all retreats on the rock face available to them (pers. obs.). Retreat temperatures were influenced by the thickness of the rock forming the roof of the particular retreat. However, utilisation of retreats by P. intermedius was poorly related to both rock thickness and retreat temperature. A consistently better relationship was found between crevice entrance height and depth and the intensity of retreat utilisation. Retreat site selection did appear to occur, with predator avoidance possibly being more important than thermal considerations in choice of retreats.

However, due to the complexity of the system and the problems involved in data collection in the field, it was difficult to ascertain which variables affected retreat choice or to assess the relative importance of these. This research project was designed to overcome many of these problems.

1. In the preliminary fieldwork, an attempt was made to estimate the number of lizards using a particular crevice by counting the number of lizards exiting the crevice in the morning for a period of two hours after the emergence of the first lizard. The number of lizards utilising particular retreats was then compared with the retreat properties. However, this method was probably inaccurate as not all individuals emerge from their crevices on a daily basis (pers. obs.). The present study is laboratory based with the focus being on giving individual animals a choice of a number of retreats differing in a single property. Social influences were thus removed.

2. It was not possible to accurately measure certain retreat properties in the field (e.g. crevice depth, temperature where lizards were actually located, roof thickness where lizards were actually located etc.) due to the uneven nature of the rock surface making up the retreat. In my study, artificial retreats are constructed according to precise measurements.

3. It was not possible to ascertain whether any movement occurred within retreats at night in the field. A range of temperatures may be available within retreats and lizards may regulate night-time Tb by changing their position within the retreat. In the present study, it is possible to monitor both position and movement within crevices accurately at night, especially with respect to the thermal gradient experiment.

4. Probably the most important aspect is that sexing in the field could only be done according to the lizard's coloration. Dissections have revealed that sexually mature males do not always have bright coloration. A more accurate assessment of sex can be made using captive animals through analysis of femoral pores, observations of breeding behaviour and dissection of the animals. Snout-vent length and weight were also taken before each experimental trial. Thus, it is possible to get a more detailed assessment of the effect of age, sex and physiological condition on retreat utilisation.

2.3 CAPTURE AND MAINTENANCE OF STUDY ANIMALS

Thirteen *P. intermedius* (five males, five females and three juveniles) were captured in May 1992 at Pullen Farm (24° 35' S, 31° 11' E). A further three lizards (two females and one juvenile) were captured in March 1993 at the same location. Males, females and juveniles were differentiated based on size, markings and coloration. The animals were caught either by hand or in net traps baited with apple at the entrance (this method being least stressful to the animals).

All lizards were transported to the Milner Park Animal Unit (WITS) where they were housed in groups of three or four in standard 3 ft aquarium tanks on a reversed day/night cycle (12D/12L). Night-time lighting from 06h30 till 18h30. Room temperature was maintained at 25-28°C and each tank was fitted with a SUN-GLO lamp to simulate sunlight. A 40 Watt light bulb was provided at one end of each tank acting as a hot spot to facilitate basking. Each tank had a layer of potting soil upon which granite slabs, providing refuges, were placed. The diet consisted of mealworms (recently moulted), crickets (when available), diced apple and tinned pet food, and was supplemented with Beefee and Calsup powder. Food and water were provided ad libitum. All lizards were weighed and their SVL measured on a weekly basis to monitor growth and assess health. Subsequent to the completion of the experimental procedure outlined in section 2.4, all lizards were released at the point of capture.

2.4 EXPERIMENTAL LAYOUT

An additional four aquarium tanks (3 ft) were used as experimental tanks. These tanks were also fitted with SUN-GLO lamps but a hot spot was not provided. Initially, Plaster of Paris was used to construct artificial retreats/crevices but cement was judged as being a better medium with which to work. A single large slab of concrete was placed at the bottom of each tank to act as a base. Crevices were created by supporting a concrete slab using polystyrene strips along three sides. Gibson, Smucny and Kollar (1989) successfully used concrete slabs surrounded by polystyrene walls and with a polystyrene layer over the roof as shelters for garter snakes in a thermal gradient study.

The first set of experiments were each designed to test the effect of a different variable (details are provided later in this chapter) on retreat selection. For these experiments, individual lizards were given a choice of three crevices. SVL and weight were recorded at the beginning of each trial. Each lizard was placed in an experimental tank at 16h30 (two hours before the onset of daytime) and observations started at 7h30 (one hour after the lizards started their night phase) the following day. This allowed the lizards ample time to explore their surroundings during daylight hours before retreating for the night. Lizards were removed from the experimental tanks at 16h30 the day after an experiment was initiated. No food or water was provided during each experimental trial as placement of these may have influenced retreat choice. The position of each lizard was recorded at three-hour intervals during their night. Each experiment was repeated five times for each lizard. For these experiments, crevice order was changed at the onset of each new experimental trial to control other biases in lizard choice. Lizards did not change positions within the crevice during their night and each night provided one data point only.

I also tested temperature preference of individual lizards using a thermal gradient. For this experiment, a single long retreat was constructed instead of separate crevices. Initially lizards were placed in the experimental tanks as in the previous experiments and their position monitored at three-hour intervals throughout the night. This revealed that the lizards did not change position during the night, making it unnecessary to continue observations for each lizard for the full 12-hour night-time period. Each lizard was then placed in the experimental tank for two hours and its position was recorded after the two hours had elapsed. As in the previous experiments, each night/experimental trial was counted as one data point only.

For all experiments, lizards were not tested in the same experimental tank on two consecutive nights in order to avoid potential bias due to the lizard being familiar with it's surroundings. Also, each lizard was left undisturbed in it's holding tank for at least two days before being used again. Furthermore, all crevices/concrete slabs were dusted off and washed down with a weak bleach solution (one part bleach: eight parts water) before the onset of each new experimental trial so as to eliminate the effect of any possible scent/faeces deposition on retreat selection by the following lizard placed in that tank. According to Cooper and Trauth (1992), very little is known about the use of pheromones in social behaviour. Pheromonal communication in lizards has long been expected and was the subject of early experimentation (Greenberg, 1943 in Cooper and Trauth, 1992). Pheromones participate in an ethological isolating mechanism and affect interspecific aggressive behaviour (Cooper and Vitt, 1987). The taxonomic distribution of pheromonal communication is largely unknown, but differential responsiveness to conspecific chemicals has been discovered in representatives of many of the lizard groups (Cooper and Trauth, 1992). *Platysaurus intermedius* do exhibit cloacal sampling (pers. obs.) and the possibility of scent deposition in retreats cannot be eliminated.

EXPERIMENT 1: CONTROL

The control experiment was performed to eliminate the possibility that other variables, not accounted for in this investigation, may influence retreat site selection. Here lizards were given a choice of three identical crevices (A, B and C). Crevice dimensions are given in table 1.

TABLE 1: Crevice dimensions for the control experiment.

CREVICE	A	B	C
HEIGHT OF ENTRANCE	10mm	10mm	10mm
ROOF HEIGHT	20mm	20mm	20mm
CREVICE DEPTH	185mm	185mm	185mm
OPENING LENGTH	250mm	250mm	250mm

EXPERIMENT 2: ENTRANCE HEIGHT

This experiment was designed to test whether lizards select retreats based on the height of the entrance (here entrance height was the same as the height within the crevice). This phenomenon may have important implications with regard to predator avoidance. Entrance height was controlled by using different heights of polystyrene holding up the concrete blocks. Dimensions are given in table 2.

TABLE 2: Crevice dimensions for crevices A, B and C used in the entrance height experiment.

CREVICE	A	B	C
HEIGHT OF ENTRANCE	5mm	15mm	25mm
ROOF HEIGHT	20mm	20mm	20mm
CREVICE DEPTH	285mm	285mm	285mm
OPENING LENGTH	250mm	250mm	250mm

EXPERIMENT 3: CREVICE DEPTH

This experiment was designed to test whether lizards select retreats based on the depth of the particular retreat. This may have important implications with regard to predator avoidance. The dimensions of the crevices are given in table 3.

TABLE 3: Crevice dimensions for crevices A, B and C used in the crevice depth experiment.

CREVICE	A	B	C
HEIGHT OF ENTRANCE	10mm	10mm	10mm
ROOF HEIGHT	20mm	20mm	20mm
CREVICE DEPTH	35mm	85mm	185mm
OPENING LENGTH	250mm	250mm	250mm

EXPERIMENT 4: ROOF HEIGHT

The height of the crevice roof may act as a visual cue indicating the approximate temperature to be expected within the retreat. Preliminary fieldwork has shown that crevice temperature is related to the thickness of the rock forming the roof of the crevice. Lizards were given the choice of three crevices differing in roof height. The dimensions of each crevice are given in table 4.

TABLE 4: Dimensions of crevices A, B and C used in the roof height experiment.

CREVICE	A	B	C
HEIGHT OF ENTRANCE	10mm	10mm	10mm
ROOF HEIGHT	5mm	20mm	40mm
CREVICE DEPTH	185mm	185mm	185mm
OPENING LENGTH	250mm	250mm	250mm

EXPERIMENT 5: TEMPERATURE

This experiment was designed to measure selected Tb of lizards given a wide thermal choice within their retreats at night. Instead of using three separate crevices, one continuous crevice was used, over which a temperature gradient was established. The dimensions of this crevice were based on the lizards choice in previous experiments selected (Table 5).

TABLE 5: Dimensions of each crevice used in the thermal gradients.

ENTRANCE HEIGHT	5mm
ROOF HEIGHT	20mm
CREVICE DEPTH	185mm

There are numerous ways in which a thermal gradient can be constructed e.g. copper heating pads (Andrews, 1994) and using heat lamps (Christian and Weavers, 1996; Christian and Bedford, 1996). For this experiment, thermal gradients were set up using heating pads and heating cables (thus eliminating any effect an additional light source may have on temperature and lizard behaviour) at the hot ends of the gradients and allowing the cool ends of the gradients to approximate room temperature. The thermal gradients were set up in a refrigerated room where the temperature was maintained at 8 °C. Two separate thermal gradients were set up (refer to figures 1A and 1B). Temperature was monitored by placing the thermocouples at intervals along the floor of each crevice. Selected temperature of lizards was measured as the temperature of the rock at mid-body of the lizard. Direct cloacal temperature measurements involve trauma to the animal (Andrews, 1994) which may affect the accuracy of the results.

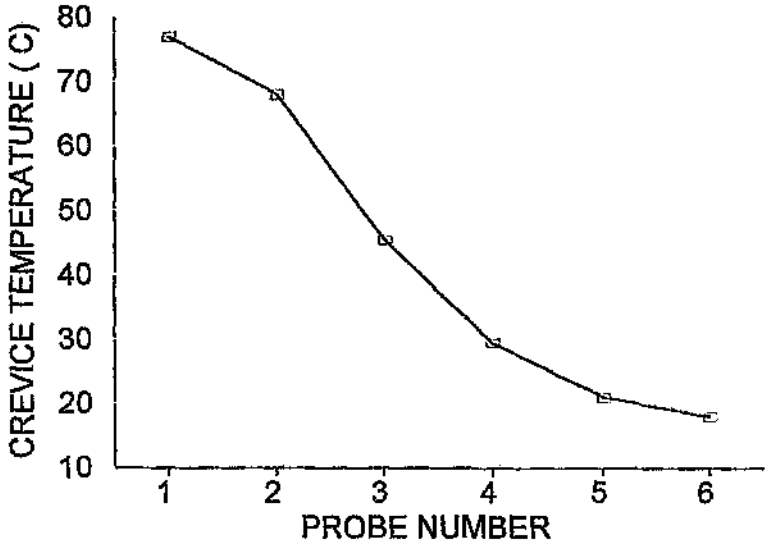


FIGURE 1A: Graph indicating temperatures available to lizards in artificially set-up thermal gradient in experimental tank 1.

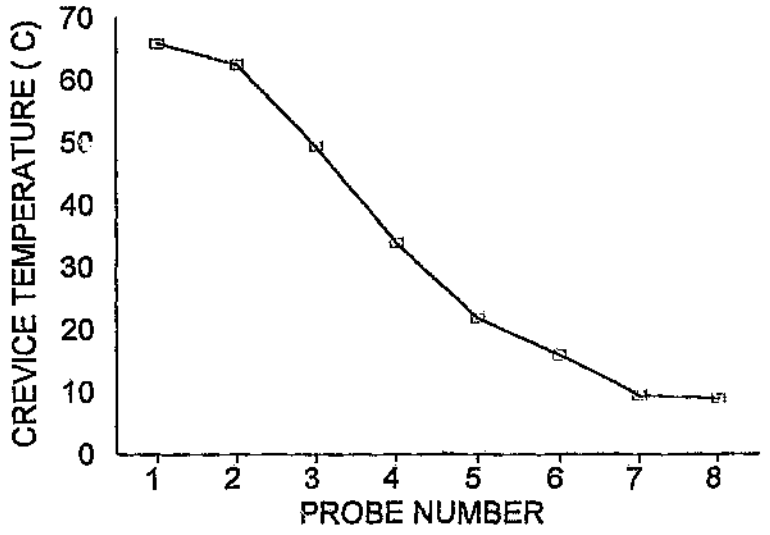


FIGURE 1B: Graph indicating temperatures available to lizards in artificially set-up thermal gradient in experimental tank 2.

2.5 FIELD WORK

For an adequate evaluation of thermoregulation, it is necessary to measure body temperature of field active ectotherms, available operative temperatures as well as preferred body temperature (Hertz et al., 1993). In accordance with these guidelines, the field work in this project entailed temperature measurements in the lizards' natural environment at night. A random selection of rock crevices was sampled. If occupied by a lizard, body temperature measurements were taken. It was not possible to measure cloacal temperature as all lizards were tightly wedged into crevices, thus lizard body temperature was estimated. The temperature reading obtained by inserting a temperature probe between the mid-body of the lizard and the rock forming the base of the retreat was used as an index of lizard body temperature. If the crevice was unoccupied, crevice temperature was measured thus allowing for investigation of the thermal consequences of selecting that habitat instead of others. Other measurements taken were air temperature and rock temperature immediately outside the retreat. These data were then analysed to test for any possible difference in body temperature achieved by lizards in the field and were compared to laboratory body temperature data. Comparisons were also made between temperature of crevices with lizards and those without.

CHAPTER 3
RESULTS

3.1 CONTROL

Chi-square tests on the results of this experiment indicate a random use of retreats by all lizards with no obvious preference for any particular retreat or position in the experimental tank (figure 3.1). The position of different lizards within retreats also varied although each lizard remained in the same position for the duration of the experimental trial.

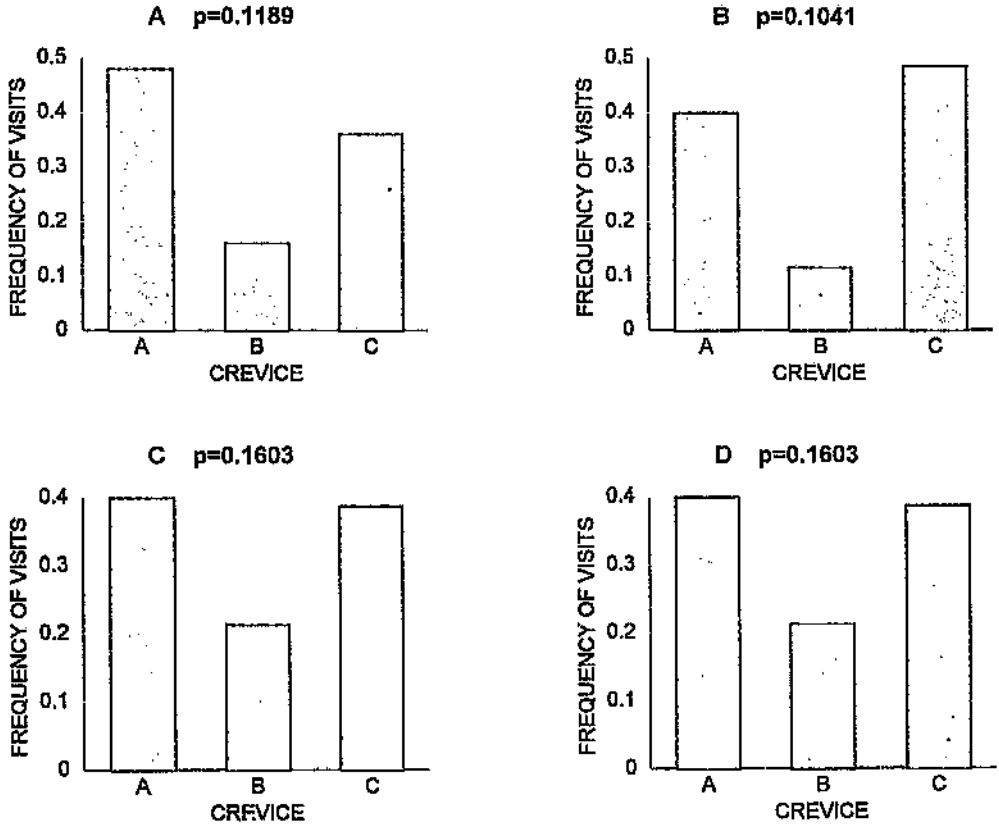


FIGURE 3.1: Graphs indicating selection frequency for crevices A, B and C by males (3.1 A), females (3.1 B), juveniles (3.1 C) and by all life history categories of lizards as a group (3.1 D). The p values refer to chi tests performed to test for a significant difference in the selection of crevices by the particular lizards.

3.2 ENTRANCE HEIGHT

All lizards selected crevice A (entrance height of 5mm) regardless of crevice order in the experimental tank indicating that crevice height is undoubtedly an important factor in retreat selection in *P. intermedius* (figure 3.2). Position within the crevice varied for different lizards but for each experimental trial, individual lizards remained in the same position throughout the night.

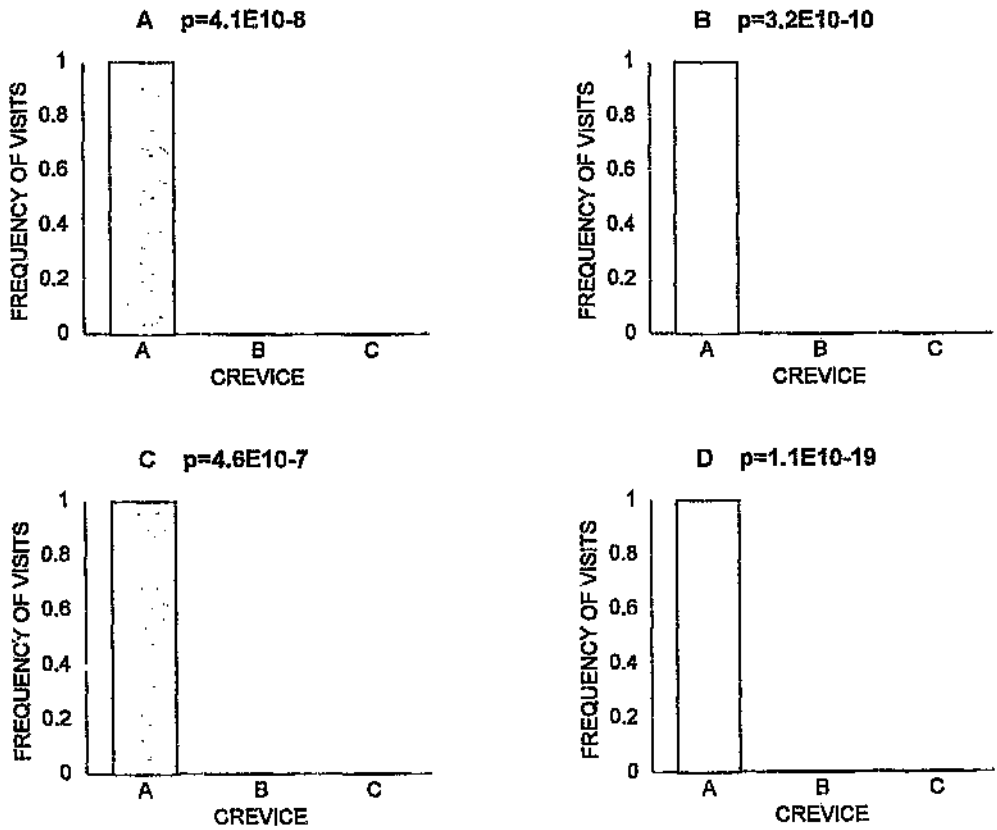


FIGURE 3.2: Graphs indicating selection frequency for crevices A, B and C by males (3.2 A), females (3.2 B), juveniles (3.2 C) and by all life history categories of lizards as a group (3 2 D). The p values refer to chi-square tests performed to test for a significant difference in the selection of crevices by the particular lizards.

3.3 CREVICE DEPTH

Again, all lizards showed a clear preference for a particular crevice (in this case, the deepest), regardless of crevice order (figure 3.3). Position within a crevice varied for different lizards (most lizards were found to curl up tightly at the back of the crevice although no clear preference for corners etc. was observed) but during any particular experimental run, individual lizards remained in the same position for the entire night.

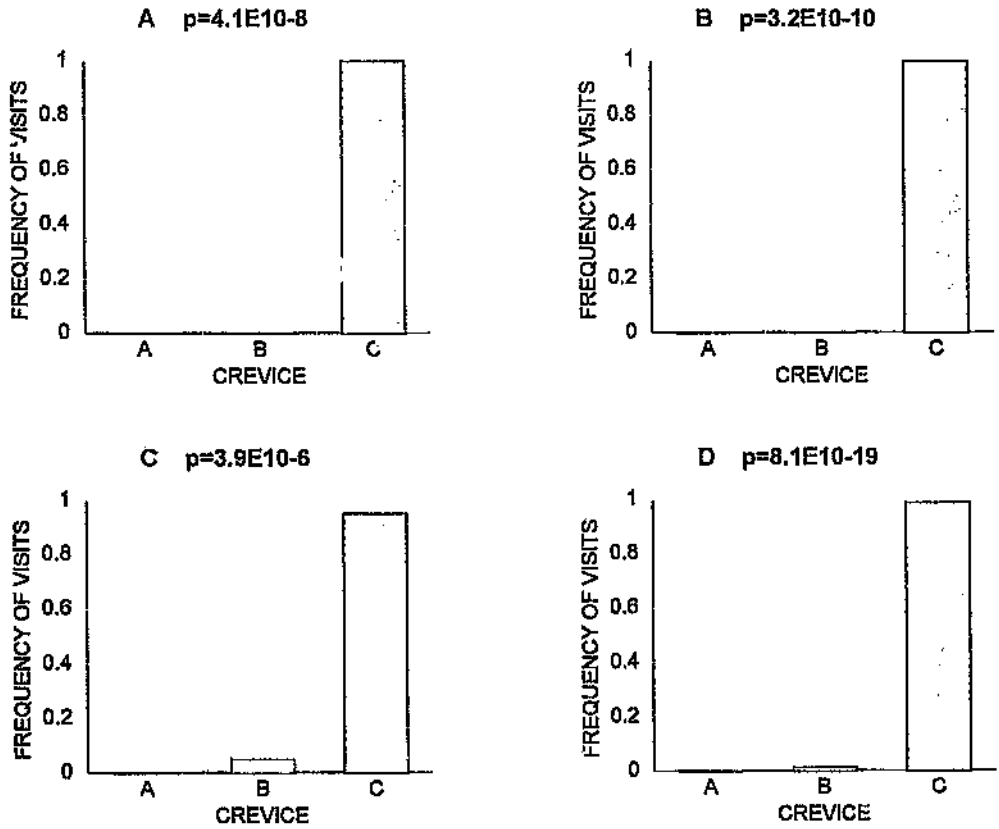


FIGURE 3.3: Graphs indicating selection frequency for crevices A, B and C by males (3.3 A), females (3.3 B), juveniles (3.3 C) and by all life history categories of lizards as a group (3.3 D). The p values refer to chi-square tests performed to test for a significant difference in the selection of crevices by the particular lizards.

3.4 ROOF HEIGHT

Chi-square test results indicate a significant difference in retreat selection (a preference for those crevices with thinner roofs) in all cases except juveniles (figure 3.4).

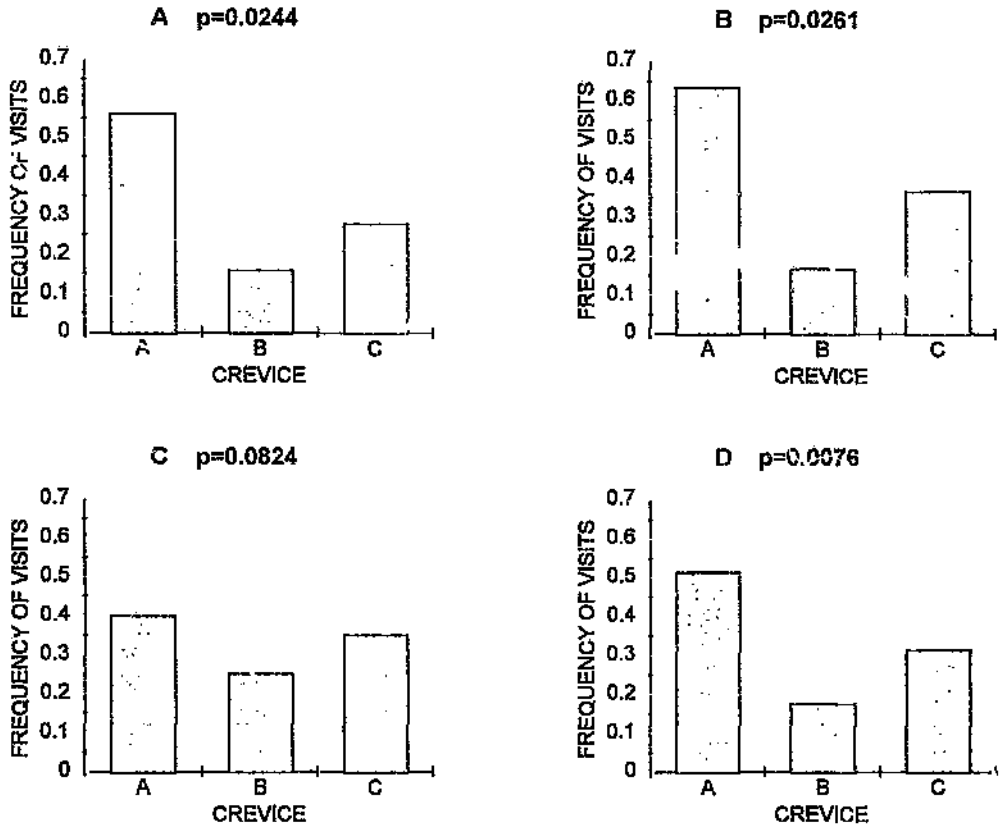


FIGURE 3.4: Graphs indicating selection frequencies for crevices A, B and C by males (3.4 A), females (3.4 B), juveniles (3.4 C) and all life history categories of lizards as a group (3.4 D). P values refer to chi-square tests performed on the results of this experiment.

3.5 TEMPERATURE SELECTION

3.5.1 LABORATORY THERMAL GRADIENT

Temperature selection results for *P. intermedius* in a laboratory thermal gradient have been summarised in table 6 and figure 3.5. Temperatures available to the lizards in the gradient ranged from 9-75°C and, as can be seen from the table, the lizards actively selected temperatures within a much narrower range of 22-43°C. An ANOVA test applied to the results of the thermal gradient experiment revealed no significant difference between the temperatures selected by lizards of different age/sex categories ($F_{2,18}$=1.79, p=0.195).

TABLE 6: Summary of the results of experiment 5 (thermal gradient). Mean temp. refers to the average temperature (°C) selected by the lizards in each category, the range indicates minimum and maximum temperatures selected and SD refers to the standard deviation of the selected temperature. Sample sizes (n) are shown in the last column.

Lizard Group	Mean Temp.	Range	SD	n
Males	32.24	22-39	2.50	5
Females	32.97	25-40	1.75	7
Juveniles	34.60	25-43	1.96	4
Total	33.11	22-43	2.13	16

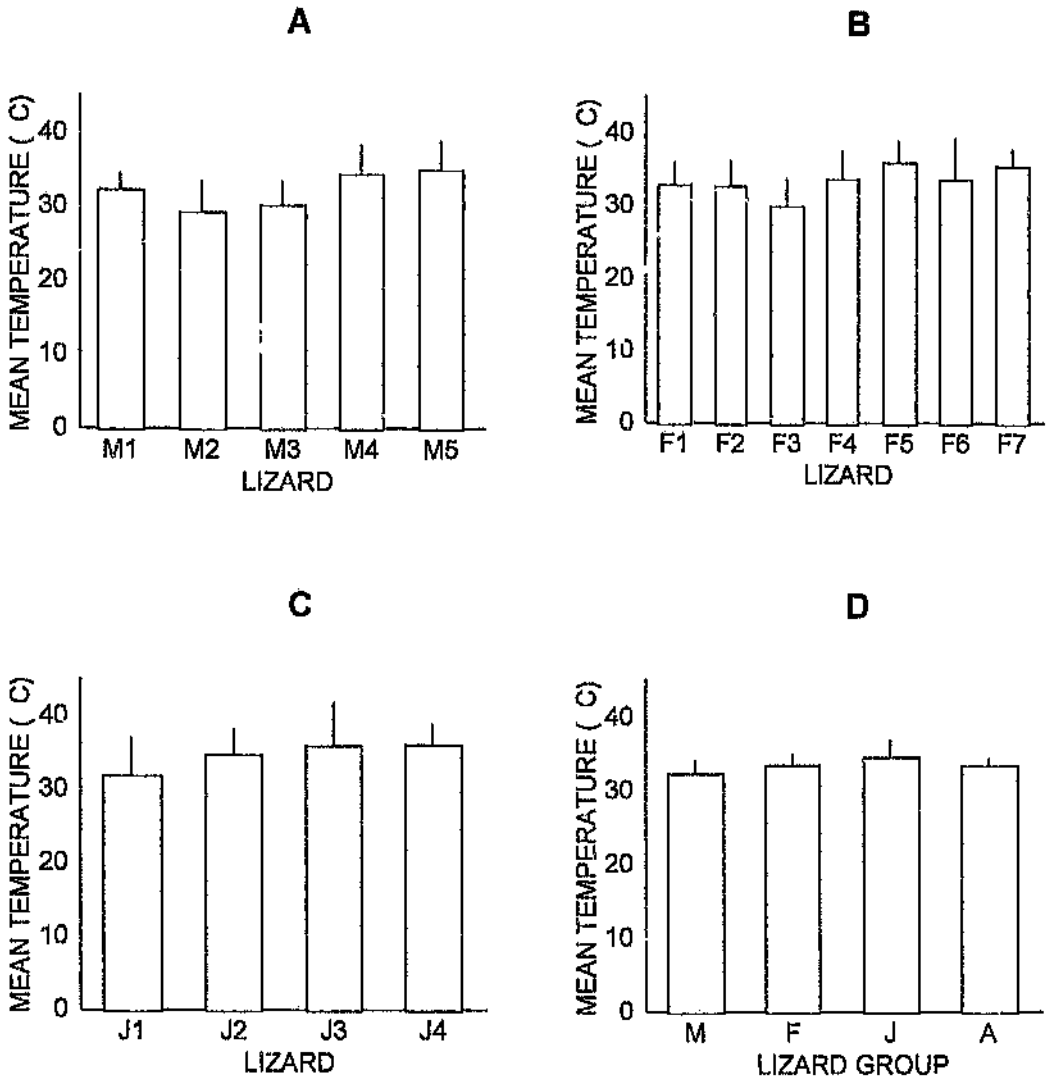


FIGURE 3.5: Graphical representation of the mean temperature selected by male lizards (A), female lizards (B), juveniles (C) and by each lizard group (D) (M: males, F: females, J: juveniles, A: all lizards combined).

3.5.2 FIELD TEMPERATURE MEASUREMENTS

Temperature measurements in the field were recorded during both summer and winter between 21h00 and 01h00 and the results are summarised in table 7 and figure 3.6. A student's t-test revealed a significant difference between temperatures of crevices occupied by lizards and those not occupied ($p = 0.028$)

TABLE 7: Summary of the results of field measurements of retreat temperatures for 29 crevices utilised by *P. intermedius* and 29 crevices unoccupied by these lizards. Maximum, minimum and mean temperatures (°C) are provided.

	OCCUPIED CREVICES	UNOCCUPIED CREVICES
MAX. TEMP. (°C)	28.6	30.4
MIN. TEMP. (°C)	12.61	11.63
MEAN TEMP. (°C)	20.66	17.93

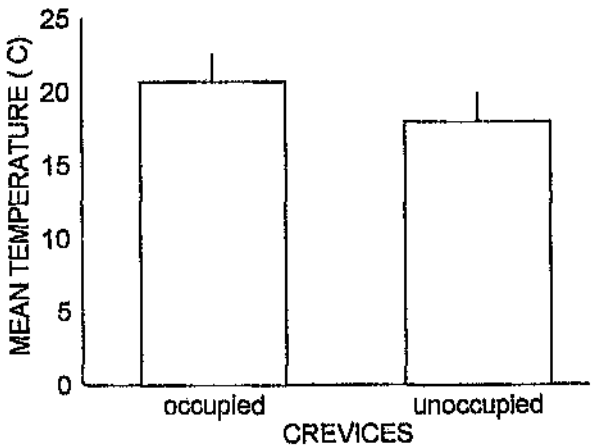


FIGURE 3.6: Graphical summary of the mean crevice temperatures (°C). 29 crevices occupied by lizards and 29 unoccupied crevices were sampled.

3.5.3 COMPARISON BETWEEN FIELD AND LABORATORY TEMPERATURE SELECTION

Temperatures available to lizards in the field ranged from 10 – 30 °C whereas the temperature range provided in the laboratory thermal gradient was 10 –75 °C. A number of variables have a potential impact on retreat choice in the field in comparison to the strictly controlled conditions in the laboratory. Thus any statistical analysis comparing the two sets of temperature measurements is hampered. For comparative purposes, temperature ranges for each were divided into groups of 5 °C, and the frequency of selection of each temperature group calculated. These data are presented in figure 3.7.

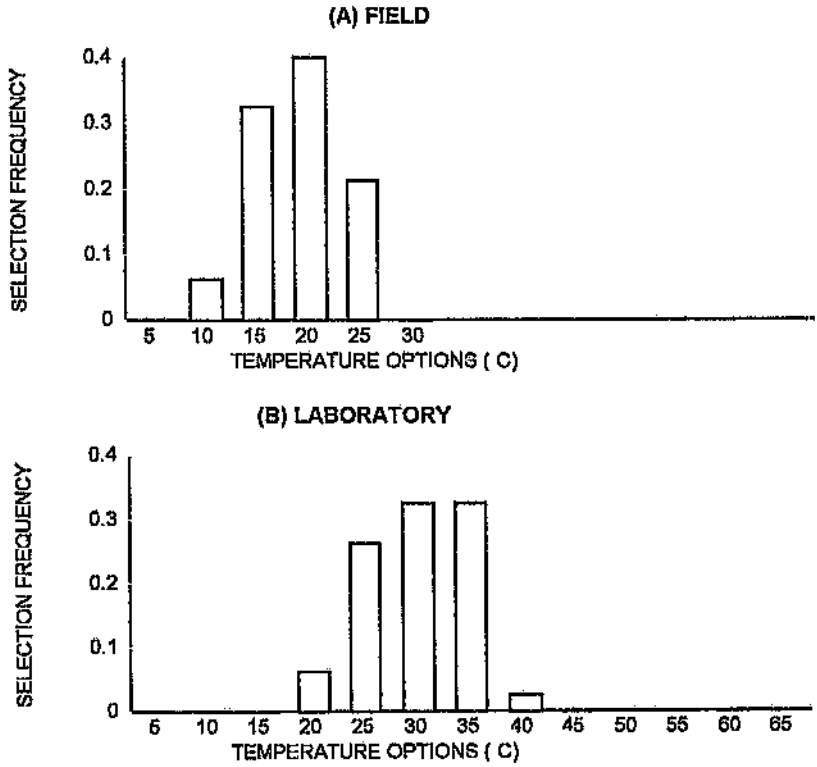


FIGURE 3.7: Graphs indicating the frequency with which lizards selected temperatures available in the field (ranging from 5-30°C) and temperatures available in the laboratory thermal gradient (ranging from 9-65 °C). Temperature ranges available have been divided into groups of 5°C, the figure indicated on the x-axis representing the lowest temperature of that particular group.

CHAPTER 4

DISCUSSION

Crevice depth and height appear to be important cues used by *P. intermedius* to assess and select retreat-sites. In my laboratory-based study, *P. intermedius* showed a significant preference for narrow crevices. All lizards selected the narrowest crevice available to them (with an entrance height of 5 mm). Similarly, when presented with a choice of three crevices of different depths, the lizards displayed a significant preference for the deepest crevice (25 mm). *Platysaurus intermedius* observed in retreats in the field had both their ventral and dorsal surfaces in close contact with the rock forming the floor and roof of the crevice respectively, and were positioned at the deepest point of the crevice. The selection of deep, narrow crevices has obvious implications with regards to predator avoidance. Deep, narrow crevices may also present an indirect cue for retreats with favourable thermal characteristics.

To ascertain the relative importance of predator avoidance in the actual selection of particular retreats, it is important to assess what predators are present and what effect microhabitat selection has on their success (Mbahinzireki et al. 1991). Although very little is known about predation on flat lizards, snakes and other lizards appear to be the main predators of *P. intermedius* (Branch, 1988) with avian predators also posing a potential threat. By selecting crevices with the narrowest entrance height in the field, *P. intermedius* lizards successfully limit their risk of being preyed upon during the period spent in retreats. The only other occupants of crevices observed in the field were spiders and other small lizards (pers. obs.). It is unlikely that either of these pose a threat to the survival of adult *P. intermedius* but spiders and scorpions are known predators of hatchling and juvenile lizards (Greene, 1988).

Another important consideration is the positioning of the lizards' body while inactive. *Platysaurus intermedius* observed in the field and laboratory generally had their tails wrapped around the body such that the tail formed a barrier between the crevice opening and the head and main body of the lizard (pers. obs.). Tail autotomy as a predator defense mechanism has been well documented (Dial and Fitzpatrick, 1981; Arnold, 1984; Arnold, 1988) and functions in reducing mortality due to predation (Congdon, Vitt and King, 1974). Flat lizards readily autotomise their tails and the positioning described above could be an effective antipredatory strategy if potential attack was diverted away from more vital areas to the tail (Arnold, 1988).

When dealing with the height of the roof of a particular retreat, my results are more ambiguous. When presented with three crevices with different roof heights, all lizards except juveniles selected the crevice with the thinnest roof (5 mm) while juveniles appear to select retreats randomly with respect to roof height. Roof height has a possible role to play with respect to thermoregulation. Preliminary field observations on *P. intermedius* showed an apparent relationship between roof thickness and crevice temperature (pers. obs.) The selection of crevices with thinner roofs may allow *P. intermedius* to initiate activity earlier as they would require a shorter time to heat up in the morning as suggested by Christian et al. (1984) without being exposed to predators. *Platysaurus intermedius* have been observed to emerge in the morning only once the rock outcrop is in full sunlight (pers. obs.).

Platysaurus intermedius of all sizes and both sexes selected unusually high Tbs (mean 33.11 °C; range 22 - 43 °C) when placed in a laboratory thermal gradient ranging from 9 - 75 °C. No significant difference in the Tb selected by lizards of different size or gender was observed. When the Tbs selected in the laboratory are compared to the temperature ranges available (11- 34 °C) and those selected (12.6 - 28.6 °C) in the field, it is clear that temperatures selected in the thermal gradient would, in most cases, be higher than those available to the lizards in their natural environment. These results appear to indicate an environmentally imposed limitation to thermoregulation to lizards in the field. However, the environmentally imposed limitation relates to crevice temperatures and it is possible that lizards are attaining a much higher body temperature during daylight hours, in full sunlight.

Field measurements revealed that the temperature of crevices utilised by *P. intermedius* was significantly higher than the temperature of crevices not occupied by them. Based on my laboratory and field observations, it appears that *P. intermedius* do use temperature as a cue in the selection of retreats although their Tb preference may be higher than temperatures available in the field.

In my laboratory experiments, all *P. intermedius* remained in the same position within a crevice for the duration of their time spent sequestered. This observation appears to suggest that the lizards assess and select a suitable retreat before entering it at night.
It is often difficult to separate the effects of selecting retreats using certain proximal cues on the animal. Although the selection of deep, narrow crevices by *P. intermedius* decreases predation risk, one must also consider the implications that the selection of retreats with certain physical properties has on thermoregulation. The choice of narrow crevices is potentially of thermoregulatory importance as an animal having both it's ventral and dorsal surfaces in contact with the rock may increase conductive heat gain (Schlesinger and Shine, 1994) or slow down heat loss. Furthermore, deeper crevices provide the animal with more shelter e.g. convective heat loss could be reduced. In my study, I was not able to conclude whether the selection of deep, narrow crevices was of thermoregulatory benefit, an antipredatory tactic or some trade off between the two.

Although laboratory measurement of Tb preference in ectotherms is widely used, results should be interpreted carefully. According to Christian and Weavers (1996), laboratory measurement of selected Tb is a valuable technique but there are problems associated with using it as a reference: An implicit assumption is that the animals in the laboratory thermoregulate by optimally exploiting the available thermal environment i.e. Tbs measures represent unencumbered, preferred Tb that they would select in an ideal habitat. But they are possibly encumbered by unmeasured stress reactions resulting in them not thermoregulating in an optimal way or they may thermoregulate optimally but have a different thermoregulatory response to artificial environment versus field (Christian and Weavers, 1996). Thus, the possibility remains that observations of lizard Tb selection in the thermal

gradient reflect an artefact of the artificial conditions imposed on the lizards in captivity. However, the lizards used in my study had already spent at least a year in captivity (with ample food, water and constant temperature conditions) before being tested in the laboratory thermal gradient and are thus unlikely to have been affected by stress during Tb measurements. My experimental group of *P. intermedius* may have become acclimatised to the new conditions and experienced a shift in temperature preference. This explanation favours the second option provided by Christian and Weavers (1996) in that my lizards displayed a different thermoregulatory response in artificial conditions.

Also, fluctuating microclimatic features such as temperature and humidity may not be used as cues for selection of retreat sites and animals may respond to these features on a local and momentary scale to obtain immediate physiological benefits (Heatwole, 1977). With an ample food supply, it would possibly be of benefit to *P. intermedius* in the laboratory to maintain a fairly high Tb to maximise, for example, digestion and, ultimately, growth. The digestive rate of many reptiles increase with Tb up to or even beyond the species preferred Tb, with an identifiable optimum temperature or temperature range (Troyer, 1987).

Structural environmental features such as retreat depth and height have often been suggested as being cues by which animals select certain habitats and microhabitats. Numerous studies have shown that animals are able to assess their habitat and make decisions based on these assessments (e.g. Brown and Brooks, 1994, Martin et al., 1991). Predation has long been implicated in the evolution of several morphological and behavioural characteristics of animals (Lima and Dill, 1989) and the selection of deep, narrow crevices has an obvious role to play with regard to predator avoidance. Predators can determine the extent of habitat use of their potential prey, an important aspect of this being the habitat features that influence predator efficiency (Mbahinzireki et al., 1991). It is logical that nocturnal retreats should offer adequate protection against predators (Clark and Gillingham, 1990). Crevice entrance height has a direct impact on the ability of a predator to gain access to the retreat. According to the crevice limitation hypothesis, narrow crevices possibly reduce vulnerability to predators since predator access is limited (Schlesinger and Shine, 1994).

Shine (1991) has discussed the crevice limitation hypothesis in relation to the environmental constraints on the prey available to blacksnakes. He found that large snakes were unable to gain access to crevice dwelling lizards. The crevice limitation hypothesis is, however, dependent on the assumption that small prey will be found in small crevices and that the available crevices are narrow enough to exclude some snakes field data on the validity of these assumptions is lacking (Shine, 1991). My data are in accordance with this hypothesis insofar as *P. intermedius* occupy the narrowest crevices possible and these are narrow enough to exclude most potential predators observed in their natural habitat. Furthermore, should a predator be small enough to gain access to the crevice, it's gape size would presumably be restricted, limiting it's ability to bite onto or engulf it's prey. However, predators need not gain access to a retreat if any part of the prey protrudes out of the crevice as they could grasp and pull it out. Thus, selection of deep crevices is obviously advantageous as it reduces predation risk further.

Huey et al. (1989) and Schlesinger and Shine (1994) showed that rock crevices with thicker roofs provided a more stable thermal environment. Garter snakes selected intermediate thickness rocks under which to retreat, allowing them to spend more time in their preferred temperature range (Huey et al., 1989). If rock crevices with thicker roofs did indeed provide a more stable thermal environment in retreats used by flat lizards, one must question why the lizards would show a preference for retreats with thinner roofs where the magnitude of daily cycles would then be greatest (i.e. the temperature would drop the most during the night). Crevices with thinner roofs allow sufficient heat to warm the lizards to penetrate the crevice faster than crevices with thicker roofs (Heath, 1962). *Platysaurus intermedius* may select crevices with thinner roofs in an attempt to heat up as rapidly as possible in the morning. Reptiles are known to warm faster than they cool, this ability existing even in very small lizards (Tracy, Tracy and Turner, 1992).

Warmer body temperature upon emergence in the morning may also have implications with regard to predator avoidance. It has been shown for a number of reptiles, that predation risk is greater at cooler times of the day and, particularly during the heating phase (e.g. Stevenson et al., 1985, Fox, 1978). Tb influences locomotor performance (e.g. Schieffelin

and DeQueroz, 1991, Hertz et al. 1982, Rand, 1964) as well as perceptive functions (Van Damme et al. and 1990, Cooper, 1994) in many reptiles. *Platysaurus intermedius* may be sufficiently warmed upon emergence from their retreats, rendering them alert and capable of detecting and avoiding predators.

The apparent lack of preference for retreats with any particular roof height in juvenile *P. intermedius* could be explained by a theory proposed by Reinert (1993) in his survey of habitat selection in snakes. He suggests that learning has a possible impact on habitat selection and cites the example of juvenile trailing of adult snakes possibly functioning as a habitat learning experience. However, this idea as well as those discussed above must remain tentative, as I have no data directly in support of them.

Furthermore, there are a number of problems with the notion that roof height is an important cue in retreat selection. Firstly, the idea that lizards select rock crevices for thermoregulatory gains based on roof thickness depends on the assumption that the lizards are able to assess by roof thickness, the expected temperature characteristics of a retreat. Also, preliminary field observations on retreat utilisation in *P. intermedius* revealed no particular preference for roofs of any height and lizards used crevices with considerably different roof thickness.

A conceptual framework to explore thermoregulation is provided by Christian and Weavers (1996) who suggest comparing Tb selected to the available thermal environment and preferred Tb in a lab gradient. In order to address the question of how carefully an animal thermoregulates, one must integrate the animals thermoregulatory behaviour, it's available thermal opportunities and the physiological and morphological properties allowing the animal to exploit it's thermal environment (Hertz et al., 1993). O'Conner and Tracy (1992) have suggested that imprecise thermoregulation may be due to limited availability of thermally suitable environments where preferred Tbs can be attained, interference with thermoregulation by other regulatory processes (hydroregulation, maintenance of energy reserves), avoidance of thermal extremes (as opposed to defence of particular Tbs) or some combination of these factors. Therefore, one must be cautious in interpreting studies of thermoregulation in ectotherms (O'Conner and Tracy, 1992).

Numerous authors have stressed the importance of comparing and attempting to match up field and laboratory observations (e.g. Castilla and Bauwens, 1991, Schlesinger and Shine, 1994). As mentioned previously, laboratory results may be artefacts of the way equipment was set up and many factors come into play and influence laboratory versus field measurements (Schlesinger and Shine, 1994). It is vitally important not to draw conclusions based on either field or laboratory results alone. An illustration of this is seen in a study on *Neoseps reynoldsi* by Andrews (1994) who concluded that these lizards showed no change in Tb seasonally from recording Tbs in spring and summer in a laboratory thermal gradient. However, this is of little significance as she did not relate his findings to field measurements and thermal constraints may change with season.

By performing suitable comparisons, Schlesinger and Shine (1994) were able to conclude that velvet geckos use a wide variety of structural, microclimatic and social cues to evaluate the suitability of alternate retreat sites and that the criteria used in captive velvet geckos generally correlate well with the types of retreat sites occupied by lizards in the field. Similarly, Castilla and Bauwens (1991) found that Tbs of *Podarcis hispanica atrata* in the field closely matched selected Tbs in a laboratory thermal gradient (Tbs that maximise running performance).

It is important to question whether thermoregulation is equally important to all ectotherms. Studies on reptilian thermoregulation have been dominated by research on small diurnal lizards living in temperate zones in environments where thermoregulatory challenges are severe (Shine and Madsen, 1996). Here, the animals devote considerable time and effort to the maintenance of high, stable Tbs and they are constrained in their times and places of activity by thermal factors (Shine and Madsen, 1996). An example of such a scenario is provided by Zimmerman, O'Conner, Bulova, Spotila, Kemp and Salice (1994), who found that in desert tortoises (*Gopherus agassizii*), microhabitat utilisation is dictated by avoidance of extreme temperatures at midday. During much of their activity season, operative temperatures were lethal for several hours during midday and the tortoises had no

behavioural or physiological resource but to eliminate surface activity and retreat to burrows where operative temperatures were more moderate (Zimmerman et al., 1994).

However, most reptiles live in the tropics where constant high temperature and high periodic annual rainfall present a unique environment for reptiles (Griffiths and Christian, 1996). Only a small number of studies have been carried out in these areas and the present understanding of seasonal ecology of reptiles in the tropics is poor (Griffiths and Christian, 1996). Although research on the seasonal ecology of tropical ectotherms has focused primarily on large reptiles (where the larger body size confers a high degree of thermal inertia), I believe similar principles can be applies to *P. intermedius*. Minimum and maximum temperature measurements at my field study site did not approach lethal limits and there was an apparent abundance of thermally distinct and easily accessible microhabitats (pers. obs.).

Under tropical environmental conditions, the ecology and behaviour of many reptiles may be affected only trivially by thermoregulatory concerns (Shine and Madsen, 1996). High, stable Tbs may be attainable through thermoconformity with no specific thermoregulatory behaviours. Similarly, consistently high environmental temperature may place few, if any, constraints on the times and places that activity can occur (Shine and Madsen, 1996).

Christian and Bedford (1996) investigated thermoregulation in spotted tree monitors (*Varanus scalaris*) in the seasonal tropics of Australia. Their results indicate that, although environmental temperatures were cooler in the dry season, the patches of sun were bigger and more numerous (due to the semi-deciduous nature of the savannah woodland) and the thermal environment did not limit the animals to low Tbs. Shine and Madsen (1996) studied water pythons in tropical Australia using radiotracking. They concluded that the pythons could easily attain suitable Tbs throughout the year without the need for costly thermoregulatory behaviour and without imposing significant constraints on spatial or temporal patterns of activity. These studies provide some evidence that opposes the prevailing paradigm that thermoregulatory "problems" are of central importance in reptile biology.

I found numerous crevices in the field with similar and sometimes higher temperatures, as well as similar depths and heights as those occupied by *P. intermedius*, to be unoccupied by the lizards. Thus, no apparent shortage of suitable microhabitats where higher Tb could potentially be attained at no added cost in terms of predation risk was observed. If "optimal" Tbs are always easily attainable, without incurring significant costs, then thermoregulation per se may be virtually irrelevant to the day to day activity of the reptile (Shine and Madsen, 1996). However, predation risk is not the only cost involved in retreat selection in *P. intermedius*. Other factors such as food availability and the potential for social interaction may play an important role in retreat selection. As mentioned previously, the thermal environment of *P. intermedius* could be limiting and crevice temperatures may not be optimal for these lizards. I would thus not say that thermoregulation is irrelevant to *P. intermedius*, but in comparison to antipredatory behaviours, it does appear to be less important.

Considering the theory of temperature space as an ecological resource (Grant and Dunham, 1988, Magnuson et al., 1979, Ruibal and Philobosian, 1970, Tracy and Christian, 1986 etc.) in relation to the points discussed above, it may be unimportant in the case of *P. intermedius*. According to this theory, "temperature space" is viewed as a partitionable, though not consumable resource and animals compete for and partition thermal resources just as they would with space or food etc. (Magnuson et al., 1979). While there can be no competition for any particular ambient temperature, the time or space in which an organism can attain optimal heat exchange can be objects of competition (Tracy and Christian, 1986). As mentioned before, there does not appear to be any shortage of thermally suitable microclimates in the study sites and thus no need for competition for these sites. However, social interactions may have an influence on the microclimates available: if, for example, a male lizard defends a number of retreats within his home range, he may thus render them unavailable to other males. "Temperature space" may, in some cases be just as important as other resources in defining territories (Tracy and Christian, 1986).

As mentioned in chapter two, *P. intermedius* are sociable lizards and males defend prime territories on the rock surface during the breeding season (Branch, 1988). Aggressive

behaviour between apparent females (it is often difficult to distinguish females from sub-adult males) has also been noted (pers. obs.) and females may also display territoriality although there is not much literature to support this contention. Although I did not test the potential effect of social behaviour on retreat and temperature selection in my study, this area is wide open for future research.

Differing microhabitat use between age classes within a population are attributable, at least in part, to thermoregulatory requirements and are due to the biophysical properties of adult and juvenile lizards (Paulissen, 1988). It has been postulated that juveniles of some lizard species may show higher selected body temperature and correspondingly different thermoregulatory behaviour to adults of the same species because of higher energy requirements for growth (Andrews and Kenney, 1990). Variation in the size of an animal may allow it to exploit different environments, which may also have an impact on Tb. An illustration of this is provided by O'Conner and Tracy (1992) who have suggested that newly metamorphosed toads (*Bufo boreas*) are able to exploit more diverse thermal environments than larger toads, due to their small size.

From my results, it is clear that the size of *P. intermedius* had minimal impact on crevice selection in the laboratory. The only significant difference found was that juvenile lizards (mass < 4g) showed no preference in the height of the crevice roof whereas adults showed a significant preference for crevices with thinner roofs. As mentioned previously, this could reflect a difference in Tb preference between adult and juvenile lizards but this contention is not supported by my laboratory observations. I found that temperatures selected by adults and juveniles did not differ significantly although this finding may have been the result of small sample sizes. Rocha and Vrcibradic (1996) have also observed a lack of significant relationship between body size and Tb in two species of skink (*Mabuya macrorhyncha* and *Mabuya agilis*) and similar observations have been reported for lizards of other families (Gillis, 1991 and Paulissen, 1988). However, few data are available to verify whether this trend is valid for lizards in general (Paulissen, 1988). Unfortunately, I experienced great difficulty in locating a large enough sample size of juvenile flat lizards in the field in their crevices. Thus, I have no field data to support the laboratory observations.

Differences in thermoregulatory behaviour and Tbs between different sexes of a species have been documented. A possible reason for this is that the differences may simply reflect differences in activity levels between the sexes (Gillis, 1991). Intersexual differences in body temperature could also be due to chromatic differences, especially in Platysaurus where males and females sometimes differ considerably in colour and ,therefore, reflective properties of the skin. Furthermore, females of some lizard species exhibit lower Tb (e.g. Beuchat and Ellner, 1987) and some exhibit higher Tb (Beuchat, 1986) when reproductive (gravid or pregnant) compared to their non-reproductive state. According to Andrews, Mendez De La Cruz and Santa Cruz (1997), two hypotheses have been invoked to account for this: 1. Thermal stress hypothesis: thermal optimum for embryos is lower than that of the female and females thus actively select lower Tb, i.e. divergent optimal temperatures for the female and for the development of her young exist (Beuchat and Ellner, 1987), and 2. Encumbrance hypothesis: females are encumbered by their clutch/litter and thus passively accept lower Tb. Andrews et al. (1997) suggest that these two hypotheses are not mutually exclusive but are complementary explanations for the thermal behaviour observed in female *Sceloporus* lizards.

No significant difference in retreat or temperature selection was found between male and female *P. intermedius* in the laboratory experiments. All female *P. intermedius* held in captivity oviposited between 06/10/1993 and 01/12/1993 and no experiments were carried out on them during this period. The possibility that gravid female lizards of the genus *Platysaurus* have different thermal regimes thus remains for future investigation.

Although *P. intermedius* is by no means a threatened lizard species, it is important to mention the implications of studies such as mine on conservation. The protection and maintenance of suitable habitat is of paramount importance for the long-term survival of wild reptile populations. To be effective, conservation and management programmes must be based on a thorough knowledge of the behaviour and ecology of the species involved (Reinert, 1993). Habitat requirements of reptiles may determine their vulnerability to anthropogenic disturbance (Webb and Shine, 1997). Basic field studies should be the first

step in any conservation programme and must be designed to produce an unbiased description of the preferred habitat as well seasonal and intrapopulational variation in habitat use patterns (Reinert, 1993).

This is illustrated in a study conducted by Webb and Shine (1997) on the conservation implications of tree hollow use by a threatened snake species (*Hoplocephalus bungaroides*). The general view regarding these snakes was that they were restricted to rocky outcrops where they use rock crevices as diurnal retreats. It has often been suggested that the reason for them being threatened is the removal of sandstone rock for use as garden ornaments. However, Webb and Shine (1997) found that most snakes moved away from the outcrops to adjoining woodland during spring where they spent long periods sequestered inside tree hollows. Tree use was found to be highly non-random with selection possibly reflecting thermoregulatory opportunities provided and/or abundance of prey (arboreal mammals) in tree hollows. They conclude that the persistence of broad-headed snakes in an area may depend crucially not only on suitable rocky habitat but also on adjacent forests.

As the above example illustrates, basic, detailed natural history studies that produce unbiased descriptions of preferred habitat and examine the seasonal and intrapopulation variation in habitat use are sorely needed (Reinert, 1993). But these require intensive fieldwork to get an adequate sample size over a meaningful time period. Hopefully, projects like mine are a step in the right direction.

CONCLUSIONS

Platysaurus intermedius show a significant preference for narrow and deep retreats. This would appear to reflect an efficient antipredatory tactic with minor potential thermoregulatory consequences. Potential predators observed in the field would be unable to gain access to these lizards during the period that they are sequestered. No significant differences in retreat or temperature selection (in the laboratory experiments) by different age groups or different sexes were observed. However, temperatures selected in the laboratory were considerably higher than those available in the field. This observation

possibly reflects an environmentally imposed limitation to thermoregulation to lizards in the field. Field recordings of lizard body temperature (when inside retreats) and the temperature of retreats not used by *P. intermedius* revealed a significant difference between the temperature of occupied and unoccupied crevices. This seems to indicate that *P. intermedius* use temperature as an environmental cue by which to select a suitable retreat. However, it is difficult to say with any confidence, whether thermoregulation or predator avoidance is of more importance to *P. intermedius* when selecting a retreat.

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