ADAPTATION TO ARIDITY IN LIZARDS OF THE *EGERNIA WHITEI* SPECIES-GROUP.

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SUMMARY

The *Egernia whitei* species-group comprises nine species, its members occupying areas of widely differing aridity in the southern two-thirds of Australia.

The adaptations to aridity of various populations within seven of the species were assessed under standardised conditions in the laboratory by measuring rate of evaporative water loss and the extent of exposure to the dehydrating conditions outside the animal's burrow or rock crevice. Both water loss and exposure varied between different populations within a species. Although the data on arid zone species were not extensive, it appeared that variability between populations was less among arid zone species.

The rates of water loss of populations from the less arid parts of any one species' range were similar. In the more arid parts, the rate of water loss was generally reduced, sometimes markedly. This pattern suggested that both genetic homeostasis and aridity control the population genotype, the former being dominant in the less arid parts of the range, the latter in the more arid parts.

There appeared to be a limit below which rate of water loss could not be reduced by decreasing skin permeability and respiratory water loss per unit body weight, and the limit was probably the same for all species. Other factors (e.g., exposure patterns) must therefore prevent the temperate and semiarid zone species occupying arid areas.

There was a tendency for the exposure of populations in the more arid parts of the temperate and semiarid zone species' ranges to be greater than exposure in less arid parts. This tendency is the reverse of what would be expected if the greater need for water conservation in the more arid parts of a species' range determined exposure, and appears to indicate that these species could not adapt to aridity by reducing exposure to dehydrating conditions in arid areas. The reasons why exposure increases in the more arid parts of these species' ranges are unknown.

In the more arid parts of their ranges, the temperate and semiarid zone species were exposed for as long as they had the

opportunity to thermoregulate - their exposure was at a maximum. The widely distributed arid zone species all showed marked restriction of exposure. Two taxa occurring in the arid zone have distributions limited to a few small localities where relief from aridity is apparently offered by high, stable burrow humidities. Both these taxa had continuous, or near continuous, exposure patterns. Restriction of exposure to dehydrating conditions appears to be essential for occupation of arid microhabitats.

The capacity of a species in the *Egernia whitei* species-group to adapt to aridity was constrained both by the inability to reduce rate of water loss below a certain level and by the inability to reduce exposure to dehydrating conditions in the more arid parts of its range.

ACKNOWLEDGMENTS

Especial thanks are accorded to the late John Mitchell, who first suggested I work on the *Egernia whitei* species-group and helped me on numerous other occasions before his death.

The debt I owe to Ken Slater will soon become evident to a reader of this thesis. The multitude of observations he made on members of the *E. whitei* species-group while he worked in the Alice Springs area have been invaluable to me. He, more than myself at the beginning of this study, appreciated the importance of his familial namesakes, *Egernia slateri* and *E. m. margaretae*.

I also wish to thank Glen Storr for the interest he has taken in my work, and for advice he has offered at different stages of the project. Terry Houston and Bob Swinbourne provided information on points of interest. I am also grateful to my supervisor, Michael Smyth, and Professor H.G. Andrewartha, who read and criticised the manuscript, and to P.I. Leppard who advised on the statistical problems involved in the analysis of data.

Finally, I wish to thank the people who have collected animals for me: Alan Butler, Brian Cooke, Brian Green, Dave Howe, Dennis King, Max King, Dave Rounsevell, Bob Sharrad and Michael Smyth.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university, and to the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

1.0 GENERAL INTRODUCTION

The *Egernia whitei* species-group comprises eight or nine of a total of about 25 species in the genus *Egernia* (Scincidae). The distributions of the members of the *E. whitei* species-group cover Tasmania and the southern two thirds of Australia. In a recent revision of the group based on external morphology, Storr (1968) wrote "One might question the validity of a species-group that embraces such diverse forms as *Egernia kintorei* and *E. pulchra longicaudata*. Yet these taxa are connected by a chain whose adjacent links are so similar as to make it hard to devise keys and diagnoses for their separation. It is this continuity in adaptation and morphology that defines the species-group rather than any characters that all its components might share.". Storr then allotted six of the eight species to two sections, each containing three morphologically very similar species. These sections were (1) the *E. whitei* superspecies, comprising *E. whitei*, *E. pulchra* and *E. margaretae*, and (2) *E. inornata*, *E. striata* and *E. kintorei*. The remaining species, *E. slateri* and *E. multiscutata*, were stated to variously combine the characters of the two sections.

The climate of the areas inhabited varies widely, from areas of 20 cm annual rainfall with a January mean temperature of about 30 C occupied by *E. margaretae*, *E. inornata*, *E. slateri*, *E. striata* and *E. kintorei* to areas of 125 cm annual rainfall with a January mean temperature of 20 C occupied by *E. whitei*. *E. pulchra* occupies areas similar to *E. whitei* while *E. multiscutata* inhabits areas slightly drier and warmer than this.

The distributions of the various species are described in S2 of this thesis. A comparison of the species distributions (Figures 3 - 10) with a map of the climates of Australia (Figure 2) shows that the distributions of many of the species in various parts of their ranges are delimited by lines connecting areas of equal aridity of climate. This suggests that the level of aridity in some way determines whether or not a species will be absent or possibly will be present in any particular area. This thesis is concerned with the factors limiting the distributions of the species in the more arid parts of their ranges, and with the adaptations allowing one species to live in an area more arid than another species. Certain species are absent from areas in which they might be expected to occur considering only the climate of the area in relation to the climates of other areas occupied by the species. Various factors could contribute to such situations (e.g., the substrate might be unsuitable), but in general these cases will not be considered in this thesis.

Adaptation to low humidities and high temperatures were selected for experimental study, these variables being most likely to be of importance to lizards in the E. whitei species-group in adaptation to arid zone conditions. The species are largely insectivorous and unlikely to suffer from low nitrogen and energy concentrations in their diets as is the case with large herbivorous mammals in the Australian arid zone (Main, 1968). Several experimental techniques were used to gain an integrated answer to the major facets of the problem:

(1) measurement of rate of evaporative water loss. This provides a measure of the potential of the animal to lose water to the environment. By comparing rates of water loss of a number of populations and species it should be possible to decide what characteristics of rate of water loss are associated with adaptation to arid conditions. However, it has been shown by Roberts (1968a) and Minnich (1970a) that the rate of evaporative water loss of reptiles increases with an increase in body temperature and a decrease in relative humidity, and the potential of an animal to lose water will be modified by its exposure to dehydrating conditions.

(2) Study of diurnal exposure patterns; exposure is taken to mean time spent by the animal outside its refuge. During a typical summer day a lizard burrow is appreciably less dehydrating than the outside environment (Minnich, 1970a; Green, 1969; and others) due to the higher humidities and lower temperatures found in the burrows. If an animal restricts its exposure to the relatively severely dehydrating conditions of the ground surface to times of the day when air, ground and its own body temperature are low and humidities are relatively high, water loss will be minimised. Diurnal exposure patterns were studied to determine if any of the species voluntarily restricts its

exposure to certain times of the day.
(3) Thermoregulation. Cowles and Bogert (1944), Heath (1965), Bradshaw and Main (1968) and others have shown that reptiles are able to avoid the lethal temperatures frequently encountered in desert areas by the selection of a cool part of their environment, this usually being a shady area, a burrow or a rock crevice. However, the possibility remains that different preferred body temperatures, or the selection of different temperatures for emergence or retreat, will influence diurnal exposure patterns. Heath (1965) found that the temperatures at which various thermoregulatory behaviour patterns were elicited varied from one species of Phrynosoma to another.

Variability of physiology and behaviour was assessed at three levels: between individuals within populations, between populations within species, and between species. Using this information, it should be possible to interpret the biogeography of the E. whitei species-group in terms of the adaptations possessed by its parts. Within any one species, variation between populations in physiology and behaviour in response to differing aridity should demonstrate some of the factors which enable one population to live in an area more arid than another population. Comparisons of the variability of, and of the limits to, adaptations within the temperate zone and the arid zone species might provide an explanation of the absence from arid areas of temperate zone species. No attempt was made to solve the problem of the absence from the temperate zone of the arid zone species.

The morphological similarities present within the sections of the species-group could reflect a recent origin of the species or older origins with correspondingly slower rates of divergence, or the existence of both alternatives within the species-group. In so far as morphology reflects the mode of life of an animal it does suggest low divergence related to ecological similarity. These similarities should facilitate the determination of some of the attributes required to persist in arid zone habitats. In comparing the adaptation of dissimilar species, for example a rodent and a lizard, so many variables would have to be taken into simultaneous consideration as to make the analysis difficult and most likely inconclusive.

The first portion of this thesis is devoted to a description of the biology and distribution of, and the microhabitats occupied by, each species. This will allow a rather more exact assessment of the stresses experienced by each species, these stresses not necessarily being directly related to the macroclimate of the area occupied by the lizard. For example, if an animal selects a moist microhabitat from the range of microhabitats available to it in any one area, the climate of that area will appear less arid than it would to an animal which selects a less moist microhabitat.

2.0 TAXONOMY, BIOLOGY AND DISTRIBUTION

2.1 TAXONOMY

Storr (1968) and Horton (1968) have provided recent taxonomic accounts of the Egernia whitei species-group, both being based on external morphology. Both presented species distributions.

Storr (1968) separated the animals into various taxa by a consideration of body proportions, scale counts and colouration. He allotted the specimens to 14 subspecies within eight species, although he considered it possible that the three subspecies of E. whitei and the two subspecies of E. margaretae should be considered as full species, and doubted the validity of dividing E. multiscutata into two subspecies.

Horton (1968) appears to have used mainly scale counts in his taxonomic treatment of the group. In most of the arid zone species the number of specimens examined was very small, and Horton's treatment of these species appears to be a restatement of that of Storr (1968). Horton differed in considering the arid zone E. slateri virgata as belonging to E. whitei. However, Horton's statement that E. s. virgata "... is completely different to the nominate subspecies." is not substantiated either by the specimen I have seen (the holotype) or by Figure 3, Plate 11 in Lucas and Frost (1896), to which Horton also refers. Horton's treatment of the E. whitei - pulchra - margaretae complex is inconsistent. His reasons for combining E. pulchra and E. whitei into one species should also have resulted in his combining E. margaretae and E. whitei (which he does not do). Horton combined E. w. whitei and E. w. tenebrosa into E. w. whitei, but Storr's reasons for separating them appear valid. Horton considered Storr's E. w. modesta to be a full species, and his reasons for this appear sufficient. With the exception of Horton's treatment of E. modesta, I have followed Storr (1968).

Both Storr (1968) and Horton (1968) listed the localities of the animals they examined. In addition, Horton gave data taken from the literature. However, he did not cite the literature from which these records were taken, and it is possible that some of the records are incorrect, being based on spurious synonomies; e.g., until Storr's work, E. margaretae was lumped with E. whitei. I have not used the data Horton took from the literature. Horton also gave distribution maps for some of the species; as localities for the occurrence of species appear on these maps which are not supported by the material or the literature he examined, they are unreliable and I have not used them. Hickman (1960) presented distribution data for Tasmania which could only refer to E. w. tenebrosa. The distribution maps shown in Figures 3 - 10 of this thesis have been compiled from locality data given by Storr (1968) and Hickman (1960), and from the locality data of the material examined personally by Horton (1968) or myself.

2.2 BIOLOGY AND DISTRIBUTION

I will preface the section on biology and distribution with some remarks on breeding, hibernation and polymorphism in the E. whitei species-group. All species produce live young, and so far as as known breeding females produce about two to three young mostly during January and February. All of the species occurring in the arid zone hibernate during winter (Slater, pers. comm.). The animals apparently do not emerge at all while hibernating. The arid zone E. m. margaretae hibernates, but the semiarid zone E. m. personata does not. Colour polymorphism exists in several species within the E. whitei species-group. I have observed it in E. whitei tenebrosa, E. p. pulchra, E. margaretae and E. multiscutata bos, and will restrict my comments to these taxa. The most striking polymorphism is in the back patterns of the abovementioned taxa, there being plain back and patterned back morphs in each. Variation in colour of other parts of the body occurs and appears to be polymorphic in at least E. whitei, but I have not examined it sufficiently to comment. The adaptive significance of the polymorphism is not known for any of the taxa. In the patterned back morph of E. whitei there is a black dorsolateral stripe enclosing a single series of pale spots on each side of the body. There is some variation in the configuration of the stripes and spots. The background colouration is usually gray, olive or copper. In the plain back morph of E. whitei, only the background colouration is present. Both patterned and plain females can produce young of both morphs. The frequency of the plain backed morph varies in different populations (from 0 to about 30%), but these variations could not be consistently correlated with any environmental features. In my experimental work, no differences between the morphs were observed in any of the variables measured. In *E. pulchra* there are plain back and stripe back animals as in *E. whitei*. In *E. m. margaretae* the pattern in the pattern back morph takes the form of a number of black markings on the back; the plain back morph lacks these markings. The situation in *E. m. personata* is not clear. In most *E. m. personata* there are some black markings on the anterior part of the back and dorsal surface of the neck which might be remnants of the dorsolateral stripe found in *E. whitei*. However, in animals from certain populations a complete dorsolateral stripe enclosing a series of pale spots can be seen, but the black pigmentation is very faint. In *E. multiscutata* plain morphs lack black pigment and are rare; patterned morphs have black pigment which usually forms a dorsolateral stripe enclosing two series of pale spots on each side of the body.

In the following pages, the place names used are shown in Figure 1. The climatic zones "humid", "subhumid", "semiarid" and "arid" are after Thornthwaite (1931) as applied to Australia by Gentilli (1948); a simplified version of the map given by Gentilli is shown in Figure 2. The information presented on the maximum attained size, refuge preference and aridity of habitats occupied is summarised in Table 2.

2.2.1 *Egernia whitei*. Distribution shown in Figure 3.

E. w. tenebrosa reach a maximum snout-vent length (SVL) of 101 mm (Storr, 1968). They occur in humid or subhumid areas on or near the coast in south eastern Australia. *E. w. tenebrosa* are found on the tops and sides of hills, in gullies, flat rocky or sandy areas and on limestone in various parts of their range. *E. w. tenebrosa* are sympatric with *E. multiscutata* at Remarkable Rocks on Kangaroo Island; *E. whitei* are found inhabiting rocky limestone outcrops, while *E. multiscutata* inhabit the sandy depressions between the outcrops. Elsewhere in its range *E. w. tenebrosa's* burrows are located beneath stones or fallen wood, where the animal either excavates a cavity between the stone or wood and the earth, or burrows into the earth itself. The burrows have two entrances (sometimes more), usually opening on opposite sides of the rock or wood. *E. w. tenebrosa* are not exposed on cold days. On warm days they are exposed during the daytime when they are seen at the entrance to their burrows or moving among rocks or vegetation. On hot days they are exposed during the morning and afternoon, but retreat to their burrows during the middle of the day. Faeces of 17 animals contained largely insect remains; some contained small amounts of plant material.

E. w. whitei reach a maximum SVL of 113 mm (Storr, 1968) and have a distribution in the humid areas of the northern coastline of New South Wales.

In all my experiments on *E. whitei*, I used *E. w. tenebrosa*.

2.2.2 *Egernia modesta*. Distribution shown in Figure 3.

E. modesta occur in the subhumid eastern interior of northern New South Wales and southern Queensland, and reach a maximum SVL of 112 mm (Storr, 1968). No experiments were performed on this species.

2.2.3 *Egernia pulchra*. Distribution shown in Figure 4.

E. p. pulchra reach a maximum SVL of 107 mm (Storr, 1968) and occur in humid areas. They live under rocks and wood.

E. p. longicaudata reach a maximum SVL of 104 mm (Storr, 1968) and occur on a number of subhumid offshore islands at Jurien Bay to the north of *E. p. pulchra's* most northerly mainland occurrence. They live among limestone (Ford, 1963) or burrow in sand.

I collected a number of *E. p. pulchra*, *E. p. longicaudata* and *E. multiscutata* in Western Australia. There were delays in the issuing of an export permit, and I had to leave the animals in someone else's care in Perth, Western Australia. The animals died either in Perth or shortly after they arrived in Adelaide.

2.2.4 Egernia margaretae. Distribution shown in Figure 5.

E. m. margaretae reach a maximum SVL of 107 mm (Storr, 1968). They are at present known to occur at five small localities in arid central Australia, where they excavate long burrows (about 80 cm) into rock crevices. Slater (pers. comm.) has examined the three Northern Territory localities, Palm Valley, Reedy Creek Rockhole and Kings Canyon. All three localities occur in water bearing rock strata, and Slater says that the nature of the surrounding vegetation (especially the presence of one or more of Livistona mariae, Ficus platipoda and Macrozamia macdonnellii) shows that this water produces high soil moisture levels; see also Chippendale (1963) for a description of the occurrence of such relic species. At Palm Valley and Reedy Creek Rockhole the water outflows to form pools. Slater (1965) has argued that these water sources have been reliable throughout the Recent Period, and his arguments are supported by the persistence of relic plant species in these areas. The situation at the South Australian localities (Piltadi Rockhole and Erliwunyawunya Rockhole) is unknown, although presumably there is free water at these localities. E. m. margaretae's currently disjunct distribution suggests that they were formerly more widespread in at least the George Gill and Musgrave Ranges; this, taken in conjunction with the high soil moisture levels in their present habitats, suggests that increasing aridity during the Recent Period has led to their extinction in all areas except those offering some relief from aridity. The long burrows of E. m. margaretae would place them in a position to benefit by a reduced rate of water loss from any source of soil moisture. When exposed, the animals are usually seen among the rocks at the entrance of their burrows. The one specimen I collected, at Reedy Creek Rockhole, had moved away from its burrow onto the surrounding rocks. K. Slater (pers. comm.) says they can be seen at the entrance to their burrows throughout the day on cool days, or during the early morning and late afternoon on hot days. The faeces from the animal I collected contained both animal and plant remains.

E. m. personata reach a maximum SVL of 107 mm (Storr, 1968). They are distributed in rocky areas in the semiarid Flinders Ranges, from 50 km north of Italowie Gorge south to around Port Germein Gorge and Telowie Gorge. Their occurrence does not appear to be dependent upon permanent water at any point in their range. Animals can be found on the tops and sides of hills and in the gullies between them and do not appear to differentiate between slopes facing in different directions. E. m. personata's refuges usually consist of a small cavity between rocks together with a short burrow (about 20 cm) dug into sand and rock debris at the rear of the cavity. The cavity forms a single, wide entrance, although additional entrances are occasionally present. On warm or hot days, animals can be seen sunning themselves in the morning at the entrance to their refuges. Later, they are found moving about among the vegetation and rocks around their refuge, and they retreat to their burrow during the late afternoon as temperatures fall. If the day is very hot, they retreat to the refuge during the middle of the day, where they can sometimes be seen with just their heads visible. E. m. personata are not exposed on cold days. Faeces collected from 29 animals at various times of the year and from various localities throughout the species' range consisted largely or entirely of insect remains, although in some animals the proportion of plant material in the faeces exceeded 50%.

2.2.5 Egernia multiscutata. Distribution shown in Figure 6.

E. m. multiscutata reach a SVL of 88 mm (Storr, 1968) and occur only on Greenly Island near Eyre Peninsula. According to Mitchell and Behrndt (1949) the animals live among rocks and fallen timber.

E. m. bos reach a maximum SVL of 94 mm (Storr, 1968). They occur in subhumid and semiarid areas on or near the coastline of South Australia as far east as Yorke Peninsula and Kangaroo Island, and in the southern part of Western Australia excluding the south west corner. E. m. bos burrow in sand in most parts of their range, although F. Mitchell and M. Smyth have informed me that they have seen them burrowing under limestone on southern Eyre Peninsula and St Francis Island respectively. The type of country occupied varies widely, from sand dune to sand plain to limestone, from relatively bare coastal foreshore to mallee scrub. From my experience of the sand burrowing populations, there is a tendency for the burrows to become deeper (up to 20 cm), for the number of entrances to increase beyond two to about ten and for the location of the burrow to shift from sand exposed to the sun to ramifying among the root system of shrubs as the area inhabited becomes more arid. *E. m. bos* can be seen throughout the day on warm days, either at a burrow entrance or in the vicinity of a burrow. The faeces of 13 animals were almost entirely composed of insect remains; occasional fragments of plant material were found.

In all of my experiments on *E. multiscutata*, I used *E. m. bos*.

2.2.6 *Egernia inornata*. Distribution shown in Figure 7.

E. inornata reach a maximum SVL of 84 mm (Storr, 1968), and have a very wide distribution in the arid and semiarid areas of Australia. Their burrows are typically located on stable sand dunes in the sand among the root system of various shrubs or tussocks (especially *Triodia* sp.; also *Casuarina* sp. and others). Near Alice Springs, Ayers Rock, Renmark and Kyancutta the burrows are shallow (about 30 cm deep) and have two or three entrances; K. Slater (pers. comm.) informs me that in the Simpson Desert the burrows are deeper (40 - 50 cm) and have numerous entrances. Slater (pers. comm.) says that on hot days animals can be seen at early morning and just after sundown; on cooler days *E. inornata* can be seen lying with just their snouts protruding from a burrow entrance throughout the day. The faeces of nine animals were examined: eight contained insect remains and the ninth also contained some wood fragments.

2.2.7 *Egernia slateri*. Distribution shown in Figure 8.

E. s. slateri reach a SVL of 93 mm (Storr, 1968). They occur in the arid zone on the alluvial fans of large rivers at a number of small, isolated localities. Although flow in these rivers is intermittent, subsurface water remains on the rocky layers underlying the alluvium at the Alice Springs locality of *E. s. slateri* (Quinlan and Woolley, 1969) and possibly does so at the other localities (Hills, 1953, records that underground water is abundant elsewhere in the area around Alice Springs especially in situations geologically similar to the Alice Springs locality for *E. s. slateri*). *E. s. slateri* dig multientrance burrows 20 - 30 cm deep which come into close contact with the tap root of *Hakea divaricata*. Observations made by K. Slater (pers. comm.) suggest that *E. s. slateri* are dependent upon an association with *H. divaricata* for survival during drought. He observed in certain areas that *E. s. slateri* burrow into the root system of *Eremophila sturtii* as well as *H. divaricata*. During a drought in the early 1960's *E. s. slateri* had a higher survival rate at a locality where there were many *Hakea* (about 90% of the burrows excavated were occupied) than at a site where there were few *H. divaricata* and many *Eremophila sturtii* (about 10% of burrows occupied). Both *Hakea* and *Eremophila* were present at a third locality, where about 80% of the burrows beneath *Eremophila* were occupied. During the last year of the drought, burrows located beneath *Hakea* were also frequently empty. During the drought, *E. s. slateri* survived best in areas where *Hakea* was abundant (even though it might have burrowed beneath an *Eremophila* at such a locality), suggesting that the water status of animals in these areas was superior to that of animals occurring elsewhere. The humidity in the air spaces in the soil around plant roots is presumably high as a result of transpiration, and *E. s. slateri's* habit of burrowing among the roots of plants suggests that *E. s. slateri* would benefit from a reduced rate of evaporative water loss as a consequence of high burrow humidities. Presumably, during drought, *Hakea* and *Eremophila* occurring in areas where *Hakea* are abundant maintain humidities in *E. s. slateri's* burrows higher than those required for survival, while in burrows located in other areas soil moisture levels have fallen too low for *E. s. slateri's* survival. *H. divaricata* occur in areas other than *E. s. slateri* localities, particularly on the plains just north of the Macdonnell Ranges. The piezometric surface of the ground water in these plains varies in depth, but may be quite shallow (Perry, Quinlan, Jones and Basinski, 1963). *Hakea divaricata* occur in low lying areas where the water table would be closest to the surface (Swinbourne, pers. comm.). *E. s. slateri's* absence from these areas is not readily explicable. It is possibly related to the fact that at *E. s. slateri* localities wind carried alluvium accumulates at the bases of *Hakea divaricata*, resulting in mounds about 10 cm high into which *E. s. slateri* burrow. On the plains north of the Macdonnell Ranges, these mounds do not form. *E. s. slateri's* distribution is apparently restricted to some of the areas where *H. divaricata* occur and where ground water is present not far below the surface. The significance of *E. s. slateri's* distribution being restricted to such areas would appear to be that the plants under which *E. s. slateri* burrow are assured a water supply more copious and stable than the rainfall in the area, and hence are able to maintain relatively high and stable humidities inside the lizards' burrows even during periods when rainfall is low. K. Slater (pers. comm.) says that *E. s. slateri's* patterns of exposure on hot and cool days are similar to those of *E. inornata*. The faeces of three specimens consisted mostly of insect remains. Some plant material was present, much of it being fragments of wood and *Hakea* leaves that would appear to have little nutritive value.

E. s. virgata have only been collected at two localities in arid central Australia. They have not been collected for more than 60 years and no details of their biology or microhabitat preference are available.

2.2.8 *Egernia striata*. Distribution shown in Figure 9.

E. striata reach a SVL of 117 mm (Storr, 1968) and are widely distributed in the arid areas of Australia. Most of the *E. striata* I have collected have come from flat sandplain in areas lacking any canopy; occasional animals have been taken from sand dunes or wooded areas. *E. striata* excavate burrows about 80 cm deep, with about ten entrances usually in and around porcupine grass (*Triodia* sp.). Two adults commonly occupy the same burrow system, and *E. striata* and *E. kintorei* are the only species in the *E. whitei* species-group in which I know this to be common. It is not known if these pairs are of the same or opposite sex. K. Slater (pers. comm.) has only observed

E. striata exposed from after sundown till 2300 hours; in my more restricted observations I have seen them exposed during the evening and also during the daytime on a couple of cool days following rain in October, 1969. The faeces of nine E. striata contained mostly insect remains (including some termites) and small amounts of plant material (mostly the seed pods of an unidentified plant).

2.2.9 Egernia kintorei. Distribution shown in Figure 10.

E. kintorei reach a maximum SVL of 206 mm (Storr, 1968). They are fairly widely distributed in the arid areas of Australia, and are sympatric with E. striata over much of their range. The burrows of E. kintorei are interspersed among those of E. striata and the two species live in the same habitat (cf., E. whitei and E. multiscutata at Remarkable Rocks, where the two species select different microhabitats: see S2.2.1). All the E. kintorei I collected came from flat, treeless sand plain. Their burrows are about 100 cm deep and have about 10 entrances opening into porcupine grass (Triodia sp.). Two adults commonly occupy the same burrow system, the members of such pairs being of opposite sex (Slater, pers. comm.). One burrow at Aileron contained seven individuals. K. Slater (pers. comm.) has only observed E. kintorei exposed from after sundown till 2300 hours. Faeces of ten animals consisted largely of insect remains (especially termites) with small amounts of lizard remains. K. Slater (pers. comm.) has identified these lizard remains as being E. striata.

2.2.10 Note on sample sizes.

Many of the sample sizes used in this study were small. A shortage of animals from numerous populations was the major factor, although a shortage of time prevented me running large numbers of animals in the behavioural experiments. In spite of this, sample sizes from most of the critical populations (the populations from the more arid parts of the various species' ranges) appear to be adequate, since variability between individuals within any one population in rate of water loss was comparatively small, and variability between individuals in

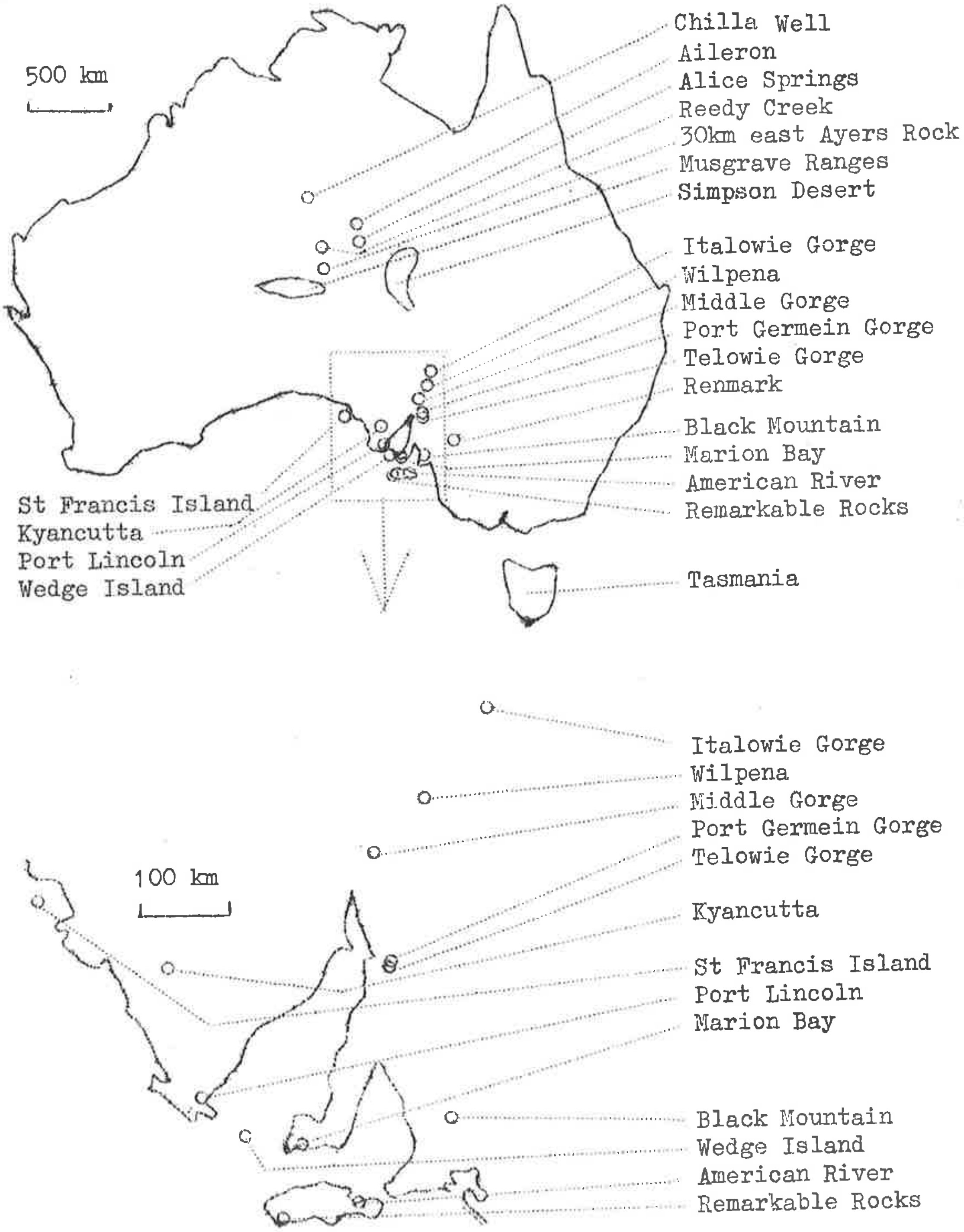


Figure 1. Location of collecting areas.

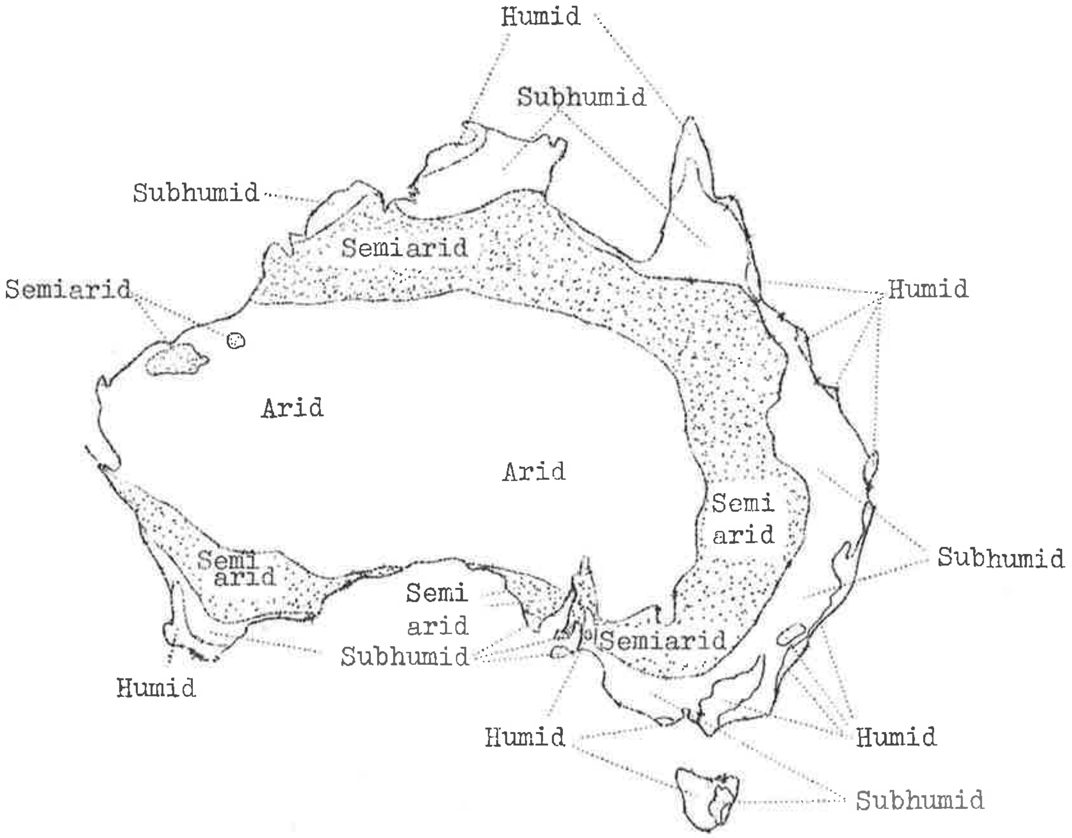


Figure 2. Simplified version of Australian climates according to Thornthwaite's system (1931). Simplified from Gentilli (1948). The climatic zones "wet" and "humid" are lumped into "humid". The classifications according to temperature and seasonality of rainfall are omitted. Approximately the northern third of the continent is classified as "hot", and the bulk of the remainder "cool", excepting some small areas in the highlands of south eastern Australia and Tasmania which are either "cool" or "cold".

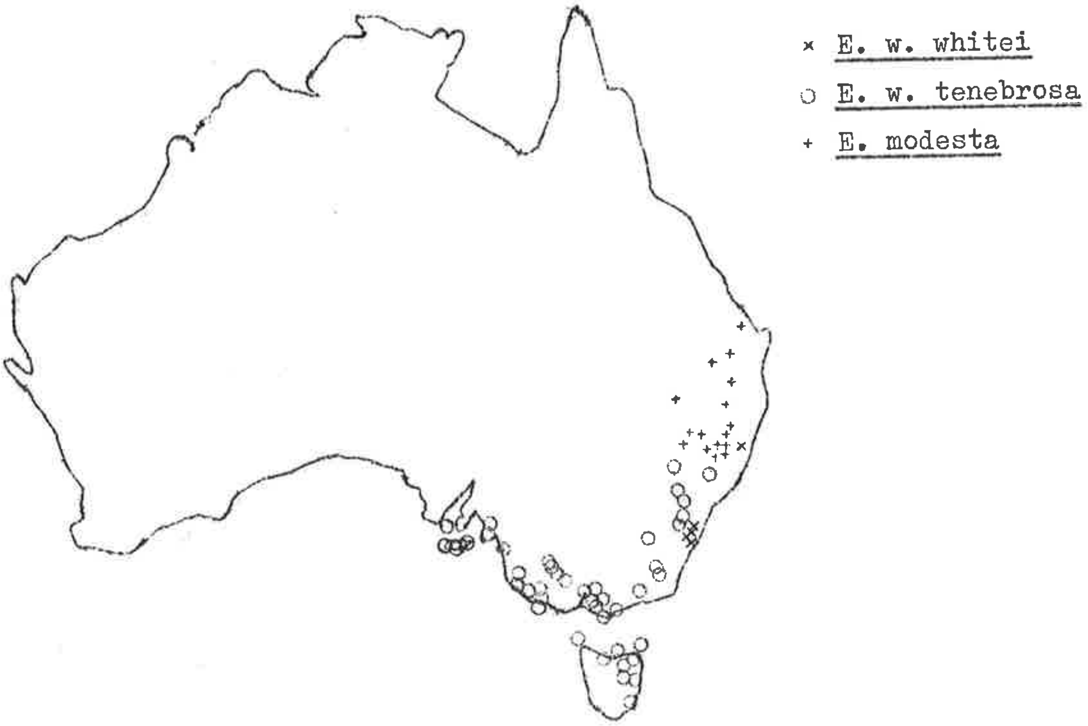


Figure 3. Distribution of Egernia whitei and E. modesta. E. w. tenebrosa is recorded as occurring on Yorke Peninsula (Marion Bay lies at the foot of Yorke Peninsula) but the exact locality in unknown and this record is not shown.

Figure 4. Distribution of Egernia pulchra.

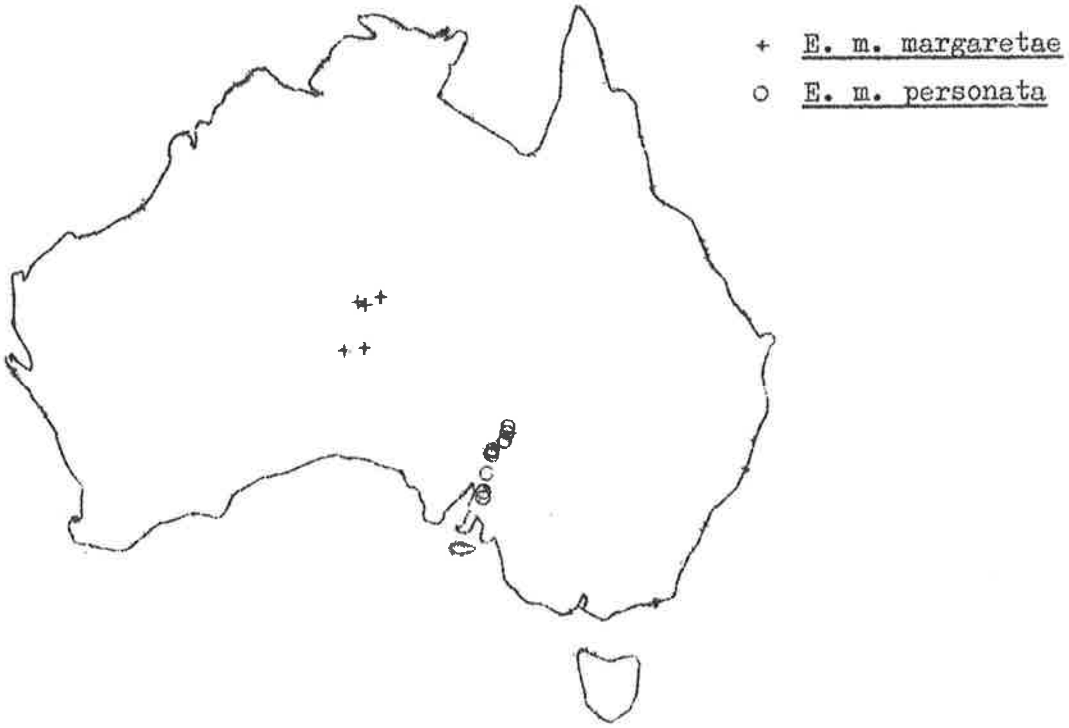


Figure 5. Distribution of *Egernia margaretae*.

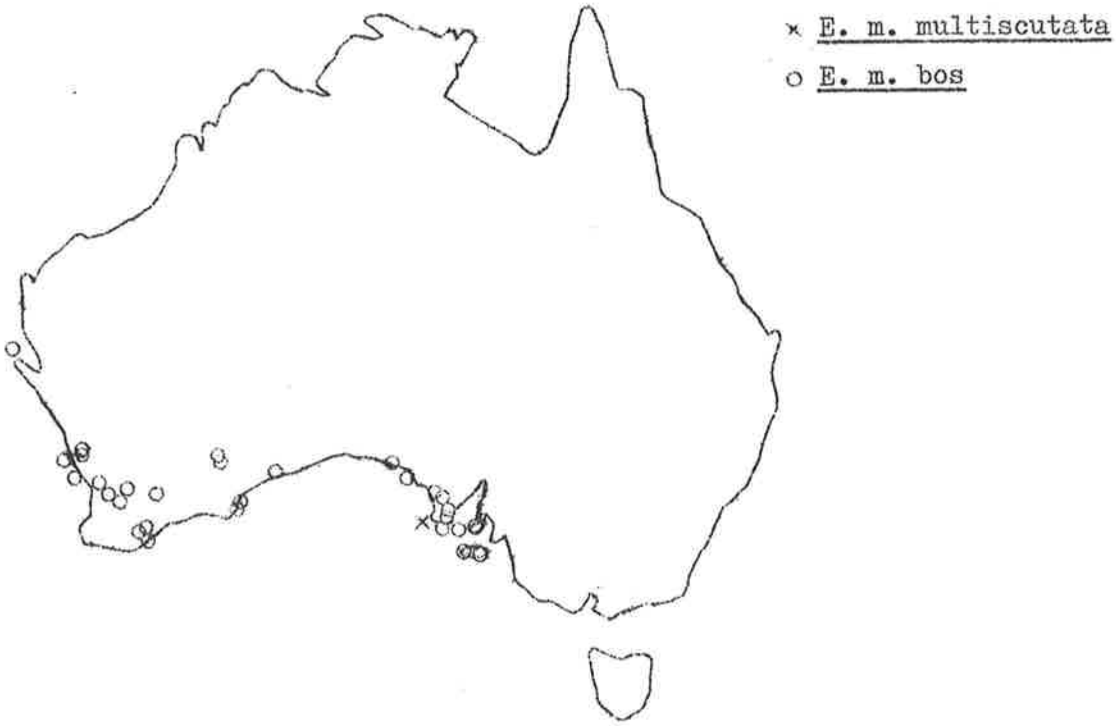


Figure 6. Distribution of *Egernia multiscutata*.

Figure 7. Distribution of *Egernia inornata*.

Figure 8. Distribution of *Egernia slateri*.

Figure 9. Distribution of Egernia striata.

Figure 10. Distribution of Egernia kintorei.

behaviour was small in populations from the more arid parts of the species' ranges, and less than in populations from less arid parts. E. m. margaretae is an exception to this statement - the rock refuges of this taxon are almost indestructible, and unfortunately only a single specimen was collected.

2.3 CLIMATE OF THE COLLECTING AREAS

2.3.1 Scope and reliability of published climatic data.

Published meteorological data will be used to develop the comparative approach used in this thesis. The microclimatic measurements I made were too few in number and scope, and taken over too short a time span, to be useful. Statistics will be considered which influence the rate of evaporative water loss of an animal on the ground surface and in its burrow, and also which influence the supply of drinking water. Statistics for January, generally the most arid time of the year, will be considered. January is also the only summer month for which relative humidity figures are readily available.

Published data are available for mean annual and monthly rainfall (Commonwealth Bureau of Meteorology, 1941, 1966), average number of rainy days per month (Comm. Bur. Met., 1966), variability of annual rainfall (Gentilli, 1971; Leowe, 1948), the probability of receiving less than a certain amount of rain in a year or in any given month (Comm. Bur. Met., 1968), three monthly and annual mean 0900 and 1500 hours relative humidity (Comm. Bur. Met., 1941), monthly and annual mean maximum, mean minimum and mean daily temperatures (Comm. Bur. Met., 1941), monthly and annual mean number of hours of sunshine, evaporation and figures for various ratios of precipitation to evaporation (Gentilli, 1971), among other things. These climatic data are collected at a limited number of localities, and the production of figures for Australia are based on extrapolation. Such extrapolation has a high probability of being accurate in central Australia, an area lacking dramatic topographical diversity and remote from the ocean, but a lower probability of being accurate in coastal areas or in areas with a high degree of topographical diversity. Fortunately, most of the collecting areas used in my study are either in areas where extrapolation is easy or are fairly close to meteorological stations. However, for some localities lacking recording stations (e.g., Wedge Island, St Francis Island) it is uncertain how much in error are the extrapolations.

2.3.2 Factors influencing rate of water loss of an animal on the ground surface.

The rate of respiratory water loss of an animal on the ground surface will evidently be determined by the difference in humidity between the inhaled and exhaled air, and by the respiratory rate and tidal volume. Measurement of the temperature of the nasal passages of a variety of vertebrates, including a lizard, Dipsosaurus dorsalis, at its preferred body temperature, has shown that the temperature of the nasal passages, and hence of the exhaled air, is dependent upon air temperature and humidity, and that as the air temperature and relative humidity increase so does the temperature of the exhaled air (Jackson and Schmidt-Nielsen, 1964; Schmidt-Nielsen, Hainsworth and Murrish, 1969; Murrish and Schmidt-Nielsen, 1970). For a lizard at a constant body temperature, it is apparent that respiratory water loss will increase both as air temperature increases and as humidity decreases. A few specimens of Egernia kintorei I dissected had nasal passages sufficiently similar to those of Dipsosaurus dorsalis (Stebbins, 1948; Murrish and Schmidt-Nielsen, 1970) as to indicate that the mechanisms for conserving respiratory water when air temperature and humidity are low present in D. dorsalis would exist in Egernia. Additionally, D. dorsalis possesses a nasal salt gland and it is probable that at least some of the water required to saturate the inhaled air derives from its secretions (Murrish and Schmidt-Nielsen, 1970). The loss of water into the inspired air is obligatory. Since its loss results in the concentration of the nasal gland secretion, the end result of nasal gland secretion is the loss from the nares of a fluid more concentrated than when it was secreted, with a consequent decrease in the amount of water lost in order to excrete a given amount of salt. Egernias also possess a nasal salt gland and I have observed salt encrustations around the nares of lizards deprived of water. The significance of salt gland secretions in maintenance of electrolyte balance is uncertain; e.g., Minnich (1970b) concluded that the salt gland contributed very little to electrolyte excretion in the desert iguana, Dipsosaurus dorsalis, while Braysher (1971) attributed a more significant role to salt gland secretions in the skink Trachydosaurus rugosus.

Respiratory water loss will be correlated negatively with absolute humidity and positively with temperature. However, as at present the mathematical nature of the relationship is unknown, precision is impossible and the most convenient forms in which data for these two variables are incorporated will be used here, these being 0900 and 1500 hours relative humidity, and temperature.

In S3.2.1 it is concluded that cutaneous water loss in a dry atmosphere and with high airflows is dependent primarily on the rate at which water can pass through the skin. In stagnant air, and as the relative humidity in the air around the skin increases, evaporation from the outside of the skin will also become a rate limiting process. The physical factors influencing cutaneous water loss have not been investigated with regard to their relative importance to animals thermoregulating in the field, but relative humidity would appear to be an approximate estimate of relative aridity.

There are few data in the literature relating to the above discussion. Measurements made on whole animals show that evaporative water loss increases as humidity decreases and as temperature increases (Roberts, 1968a; Chew and Dammann, 1961). From the temperature of the nasal passages of Dipsosaurus dorsalis held at a constant body temperature, Murrish and Schmidt-Nielsen (1970) inferred lower rates of respiratory water loss in cool air than in warm air. It would appear that no one has measured the rate of water loss of a lizard with a body temperature other than air temperature.

The foregoing discussion on the rate of water loss of an animal on the ground surface makes no allowance for the thermoregulatory behaviour of reptiles. In the areas considered here, this behaviour will not alter the relative aridity to diurnal reptiles of areas already judged arid. A lizard may gain heat by conduction from the air and ground or by radiation falling directly on the lizard. For any given body temperature when the flux from radiation is high that from conduction will be low and vice versa (see Porter and Gates, 1969, for a discussion of the relationships between radiation levels, air and ground temperatures, and body temperature). Because, with absolute humidity constant, hot air is dry air in the sense that it promotes greater evaporation, a lizard will lose least water when it attains its preferred body temperature with radiation at a maximum. Consequently the time of the day at which the lizard is exposed influences its liability to desiccation. For example, assuming animals are at their preferred body temperature, the high maximum air temperatures in central Australia impose a dawn and dusk exposure pattern on diurnal animals. Minimum January air temperatures at night are higher in central than in southern Australia, and exposure at dawn would occur in the presence of higher air temperatures and lower radiation levels in central than in southern Australia. Exposure at dusk would occur in the presence of low radiation levels and hence high air temperatures. Conversely, exposure in southern South Australia would occur more in the daytime, and consequently at times with higher radiation levels and hence lower air temperatures than exposure in central Australia. From this rather theoretical discussion it appears that in an area where the measured aridity is high, the area's aridity to diurnal reptiles is also high. Exposure at night, found in the field with Egernia striata and E. kintorei, occurs in the presence of cooler air and at body temperatures below the level preferred in a thermal gradient, thereby reducing the rate of evaporative water loss (Roberts, 1968a; Murrish and Schmidt-Nielsen, 1970). Norris (1967) has presented a detailed discussion of the variables influencing heat transfer between a lizard and its environment. He also discussed metabolic heat production and evaporative water loss, these two variables influencing a lizard's body temperature in ways other than by altering conduction, reflection, or radiation of heat from the surface of the lizard. However, insufficient information exists at present concerning the physical environment at the localities from which Egernia were collected to allow a fruitful application of Norris's approach to Egernia habitats. Much of Norris's discussion revolves around the significance of colour change in heat transfer, and it is appropriate at this point to mention that none of the Egernia whitei species-group appears to undergo any change in colour in response to temperature, stress or breeding condition.

2.3.3 Factors influencing rate of water loss of an animal in its burrow.

The problem of rate of water loss in the burrow is more complex and involves the determination of both the burrow temperature and humidity in that part of the burrow occupied by the lizard. Evidence is presented in S4.3.2.3 suggesting that animals in the laboratory will thermoregulate at their preferred level in their burrows during the daytime, though they would not have the opportunity to do so for most of the night. It is possible that they would also thermoregulate in their burrows during the daytime in nature. Diurnal changes of humidity and temperature gradients in the burrow, as well as differential usage of different parts of the microclimatic spectrum available to the animal in its burrow, make any attempt to predict quantitatively the results of this interplay during the daytime unrealistic, even if one assumes that the animal will be at its preferred body temperature. During that part of the night spent by the lizard in its burrow, it presumably retreats to the bottom of its burrow. The number of variables affecting soil temperature and humidity is so great as to in all probability render any attempt to predict the values of these parameters spurious. From the few measurements that were taken burrows in the arid zone appear to be warmer in their coolest part (about 30 C) than burrows or rock crevices in the temperate zone (20 - 25 C). Burrow humidities were not measured in this study. Other workers have found that burrow humidities even in arid areas are generally fairly high (85%:

Green, 1969; 60%: Minnich, 1970a) although fairly low values have been reported by Warburg (1964) (30 - 40%) and Schmidt-Nielsen and Schmidt-Nielsen (1950) (30%). However, none of these measurements considers the influence of the animal itself in humidifying its own burrow. Humidities at the bottom of burrows would probably be high in temperate areas and in arid areas where the animal digs deep burrows, although they would be expected to fall during drought. Egernia slateri and E. m. margaretae are two species where special circumstances exist, and they have already been discussed (S2.2.4 and S2.2.7).

2.3.4 Factors governing the supply of drinking water.

Since all species in the group drink in the laboratory, and I have observed Egernia striata drinking in the field, the frequency with which rain falls might be important to an animal's water balance. Data for the number of days without rain during drought are not available. Rainfall is highly erratic in central Australia (Gentilli, 1971, Figure 32) and mean values are of little use in determining stresses likely to be encountered. The only data available for number of rainy days per month are mean values. Figures for the amount of rain at or below which it can be expected that a certain percentage of all observations will occur appears to be the only form in which the variability of precipitation for below average rainfall is incorporated (Comm. Bur. Met., 1968). The appropriate figures in Table 1 are taken either from the tables in Part1 or from the graphs in Part 2 of this reference. It is evident that although the 50 percentile January rainfall in central Australia is comparable to, or greater than, that of southern South Australia, the 10 percentile rainfall is generally lower at the localities considered here. Data for winter rainfall are not presented, but much less rain falls in central than in southern Australia during winter.

Dew is likely to be a potential source of drinking water in coastal regions. In the arid zone, however, dew falls only during and for a few days after rain (Slatyer, 1962) and would not be significant as a source of water.

2.3.5 Climatic data for the collecting areas.

Comparative climatic data for localities where lizards were collected for this study are shown in Tables 1 and 3. It is evident that the central Australian localities are hotter and less humid than the southern Australian localities.

In some cases where the aridity of two habitats is compared, it is difficult to decide from Table 1 which is the more arid. The cases relevant to this thesis are Marion Bay and St Francis Island (both *E. multiscutata* localities), and the *E. whitei* localities (Remarkable Rocks, American River, Black Mountain and Wedge Island). In January, St Francis Island is about as hot as, slightly more humid than, but receives slightly less rain than Marion Bay. Additional climatic data are shown in Table 3 for these two localities, and show that during the other summer months St Francis Island is more arid than Marion Bay. Considering the *E. whitei* localities, Remarkable Rocks is less arid than American River which is less arid than Wedge Island. However, the position of Black Mountain is far from clear. Wedge Island is cooler, more humid, but receives appreciable less rain than Black Mountain in January. These same differences exist in all the summer months. *A priori* it is not possible to decide whether Wedge Island is more or less arid than Black Mountain, although the experimental data obtained from *E. whitei* collected from these two areas suggest that Wedge Island is more arid than Black Mountain. Accordingly, Wedge Island is shown as being more arid than Black Mountain in Table 2. Since Remarkable Rocks and American River are both cooler and more humid than Wedge Island, the differences between these two localities and Black Mountain are more accentuated than they are between Black Mountain and Wedge Island. In addition the rainfalls at Remarkable Rocks and American River are closer to that of Black Mountain than is the rainfall of Wedge Island. It would seem that Black Mountain is more arid than either Remarkable Rocks or American River.

Table 1. Comparative meteorological data for January for the localities from which *Egernia* were collected. See Figure 1 for distribution of localities, and text for sources of information.

Locality	Species collected	Temp (C) Mean max	Temp (C) Mean daily	Relative humidity 0900	Relative humidity 1500	10% ile rain (mm)	50% ile rain (mm)
Chilla Well	*E. striata*	36	31	38	24	2.5	38
Aileron	*E. kintorei*	36	30	35	22	0.0	23
3 km south of Alice Springs	*E. slateri*	36	29	30	22	0(a)	15
Reedy Creek	*E. m. margaretae*	36	30	30	22	0(a)	11
50 km south of Alice Springs	*E. inornata*	36	30	30	22	0(a)	12
30 km east of Ayers Rock	*E. inornata*	36	30	30	22	0(a)	7.6
Renmark	*E. inornata*	31	22	45	29	0(a)	8.4
25 km SSW of Kyancutta	*E. inornata*	27	22	50	45	0(a)	6.1
Italowie Gorge	*E. m. personata*	34	28	35	24	0(a)	4.8
Wilpena	*E. m. personata*	33	26	37	27	0(a)	7.6
Middle Gorge	*E. m. personata*	33	25	38	30	0(a)	8.9
Port Germein Gorge	*E. m. personata*	31	24	42	33	0.0	10
Telowie Gorge	*E. m. personata*	31	24	42	33	0.0	10
St Francis Is	*E. multiscutata*	24	21	60	52	0(a)	5.1
Marion Bay	*E. multiscutata*	25	19	57	50	0.2	6.8
Remarkable Rocks	*E. multiscutata* and *E. whitei*	23	18	65	56	2.0	10
Wedge Island	*E. whitei*	26	20	56	54	0.0	7.6
Black Mountain	*E. whitei*	28	21	50	40	2.5	10
American River	*E. whitei*	24	18	67	53	0.3	8.5

(a) signifies that no rain falls during January in more than one year in ten.

Table 2. Summary of maximum attained size, refuge preference and range of habitats occupied by the members of the *E. whitei* species-group used in this study. In those species from which more than one population was sampled, the localities are arranged sequentially in order of increasing aridity. Localities shown in Figure 1 and their climates in Table 1. The horizontal line in the "Range of climates occupied" column below the categories "humid", "subhumid" etc. indicates in which categories the species occurs. Abbreviations listed below.

Species (max SVL in mm)	Refuge preference	Range of climates occupied (1)			
		Humid	Subhumid	Semiarid	Arid
E. whitei (101 mm)	Rock	———	RR AR BM W		
E. m. margaretae (107 mm)	Rock				(2)
E. m. personata (107 mm)	Rock			PG MG W IG	
• • • • • • •	• • • • • •	• • •	• • •	• • •	• • •
E. multiscutata (94 mm)	Sand		RR	MB SF	
E. inornata (84 mm)	Sand			K R	AS
E. slateri (94 mm)	Sand				(2)
E. striata (117 mm)	Sand				———
E. kintorei (206 mm)	Sand				———

(1) Climatic zones according to Thornthwaite (1931). Elsewhere in this thesis, the humid and subhumid zones are usually referred to as temperate.

(2) Although this species is listed as occurring in the arid zone, it is uncertain if its microhabitat is arid - see S2.2.4 and S2.2.7.

Abbreviations:

E. whitei RR = Remarkable Rocks AR = American River
BM = Black Mountain W = Wedge Island

E. margaretae PG = Port Germein Gorge MG = Middle Gorge
W = Wilpena IG = Italowie Gorge

E. multiscutata RR = Remarkable Rocks MB = Marion Bay
SF = St Francis Island

E. inornata K = Kyancutta R = Renmark
AS = Alice Springs

Table 3. Climatic data for St Francis Island and Marion Bay for the months October to April. See text for sources of information. Humidity data are only available at three monthly intervals. Rain in mm, temperature in C.

	Marion Bay							St Francis Island						
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Oct	Nov	Dec	Jan	Feb	Mar	Apr
10% rain	11	2.8	1.0	.25	.51	2.0	6.3	6.1	.51	.25	0(a)	0(a)	.51	3.3
50% rain	35	18	12	6.8	6.8	8.6	28	19	13	7.6	5.1	4.6	7.6	18
RH 0900	62			57			68	55			57			65
RH 1500	65			50			60	50			52			55
Mean temp	14	17	18	19	20	18	16	16	18	20	21	21	20	17
Max Temp	19	22	24	25	25	23	20	22	23	24	24	25	24	23

(a) signifies that no rain falls during that month in more than one year in ten.

2.4 MAINTENANCE OF ANIMALS

Lizards were usually kept at room temperature in containers with up to three animals of other species. The containers were about 30 cm deep by 60 cm by 30 cm. Sand deep enough for the animals to burrow and rocks were placed in the bottom. Animals were given water and fed mealworms (larvae and adults), bananas and occasionally other insects. Heat and light were supplied on a 12 - 12 photoperiod, although some animals did not receive heat for up to several weeks at a time. Some animals were kept in a 27 C constant temperature room. The lizards appeared to be healthy and mortality was low.

3.0 RATE OF EVAPORATIVE WATER LOSS

3.1 INTRODUCTION

The amount of water an animal loses by evaporation will be determined by two variables: the extent to which the animal exposes itself to dehydrating conditions, and its potential to lose water when placed in dehydrating conditions. The animal's potential to lose water can be readily determined in the laboratory by measuring the rate of water loss when the animal is exposed to known conditions. Many workers have made such measurements on reptiles under a variety of conditions of temperature, relative humidity, previous thermal history, duration of measurement and whether the animal is in a dark or light environment (Bogert and Cowles, 1947; Chew and Dammann, 1961; Dawson, Shoemaker and Licht, 1966; Claussen, 1967; Gans, Krakauer and Paganelli, 1968; Roberts, 1968a; Sexton and Heatwole, 1968; Green, 1969; Bradshaw, 1970; Minnich, 1970a; and others). The generalisation has emerged that xeric species lose less water by evaporation than mesic species. Although Bradshaw (1970), Gans et al. (1968) and Sexton and Heatwole (1968) have compared taxa related at the generic level, no one appears to have presented data for variability between populations within a species.

The potential to lose water by evaporation will be the sum of cutaneous and respiratory water loss, and since activity will alter at least respiratory water loss by increasing minute volume, its influence as a variable must be considered when interpreting rate of water loss measurements (Roberts, 1968a; Sexton and Heatwole, 1968; Minnich, 1970a). Where activity has been considered in previous studies, it has usually been assumed that an increase in rate of water loss in the absence of excretion and moulting is a consequence of activity. Moulting transiently increases the rate of evaporative water loss (Gans et al., 1968). In my study I tried to eliminate the influence of activity on rate of water loss measurements I used to compare different individuals. Activity of animals in the field occurs usually as a result of foraging for, and the irregular appearance of, food items; to a thermally diverse environment, to the presence of predators or animals of the same species and probably to other components of the environment. Although levels of activity inferred from water loss experiments obviously represent the animals' tendencies to be active under the conditions used, containers as simple as those used in water loss experiments would be most unlikely to elicit activity levels comparable in any way to activity levels occurring in response to the varied components of the environments lizards experience in nature. My experimental technique and procedures for the selection of measurements from the data obtained were therefore designed to facilitate elimination of the influence of activity on rate of water loss.

3.2 METHOD

3.2.1 Experimental technique.

Roberts (1968a), Green (1969) and Braysher (1972) have shown that to obtain minimal values for rate of water loss in diurnal lizards it is necessary to measure the rate of water loss at night and in complete darkness. Presumably activity is at a minimum at such times. Although Roberts (1968a) found no change in measurements made on successive nights, the data presented by Bogert and Cowles (1947) show that the rate of water loss probably decreases over successive days in at least some reptiles. The apparatus for my work was designed to allow continuous measurement of rate of water loss during the day and night over a number of days without disturbing the animal, and in complete darkness at night. Water loss was measured directly rather than as weight changes of the animal in order to avoid assuming that the animal was metabolising fat, where the weight loss in carbon dioxide production equals the weight gain in oxygen consumption. The apparatus is illustrated in Figure 11. Compressed air was fed through two large jars of CaCl2, through a smaller jar of Mg(ClO4)2 and then into a 27 C constant temperature cabinet where it passed through a copper coil to equilibrate the temperature of the ingoing air with that of the cabinet. The air flow was then split into three channels, each portion passing through two U tubes containing Mg(ClO4)2, through a chamber containing the animal and then through another two or three U tubes containing Mg(ClO4)2. The

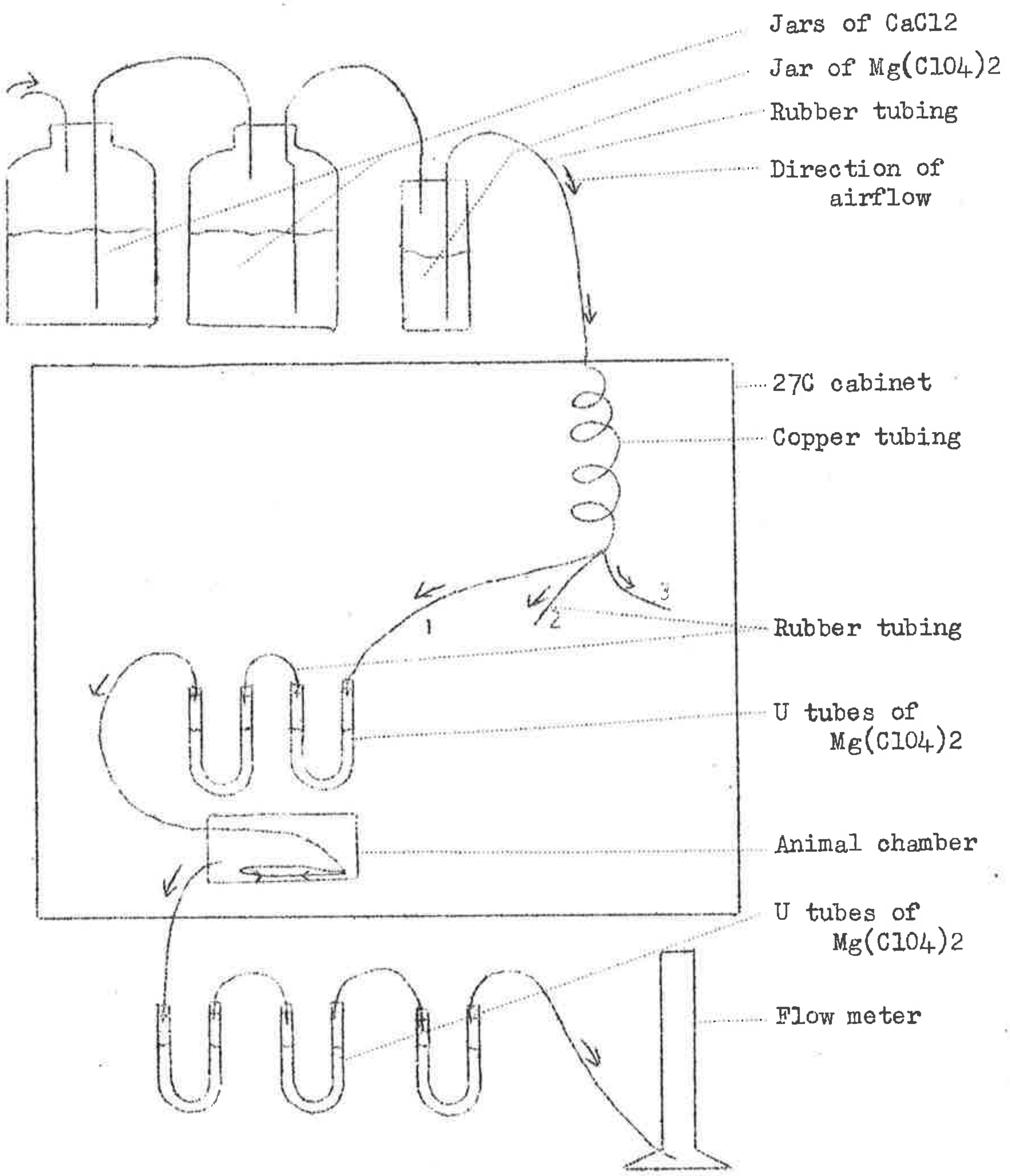


Figure 11 . Apparatus for measuring rate of evaporative water loss. After the point at which the airflow is trifurcated, only one of the three trains is shown.

final series of U tubes was outside the cabinet so the tubes could be weighed without disturbing the animal, this measurement giving the rate of water loss of the animal. The rate of air flow was measured by a flow meter after the final series of U tubes.

Smoke testing of the chambers showed that there were no stagnant pockets of air in the animal chambers. Tubes of desiccant were marked and always oriented in the apparatus the same way; during water uptake a water content gradient was set up along the tube and if the U tube were to be reversed the excurrent air would have a high humidity, leading to an error in measurement of rate of water loss if this tube were the last in the train. The uptake of water by the CaCl2 led to changes in the texture of the desiccant which were clearly visible. When the desiccant in the leading jar was exhausted, the trailing jar became the new leading jar and a trailing jar containing new desiccant was inserted. The predrying U tubes were weighed regularly and replaced if the second tube had taken up a significant amount of water. The same sequence of rotation was used for the predrying tubes, and also for the postanimal tubes, as for the jars of CaCl2.

The rate of water leakage into the system was checked by running the setup without any animals. Leakage rates varied from 0.3 - 1.0 mg/hr, usually being in the range 0.4 - 0.6 mg/hr. As the variation in the leakage rate could account for a large proportion of the day to day variability in minimum values, 0.4 mg/hr was subtracted from the minimum value obtained when the animal was in the chamber, it being reasoned that the measured rate of water loss would most probably be at a minimum when the rate of leakage was at a minimum. In the absence of the excretion of faeces or uric acid pellets, and allowing for a leakage rate of 0.5 mg/hr, the sums of the measured water losses were usually slightly less than the weight losses of the animals. This could mean either that the respiratory quotient was greater than 0.7, or that in actual use the rate of leakage into the apparatus was less than 0.5 mg/hr.

Using Mg(ClO4)2 as a desiccant, it is extremely unlikely that errors would be introduced into the measured rate of water loss as a result of the predrying and postanimal tubes being at different temperatures: predrying at 27 C, postanimal at ambient. While it is possible that the efficiency of the desiccant changes with temperature, these changes would have to be enormous to introduce a significant error. No evidence was obtained to suggest that this might be the case. It appeared that a more significant source of error was the influence of atmospheric humidity on the Mettler balance during the early water loss runs; this error was minimised during later runs.

Unsuccessful attempts were made to partition water loss into cutaneous and respiratory components by the use of an apparatus designed to separate water loss from the head from that of the body (the apparatus was similar to that described by Claussen, 1967). However, the animals persisted in violent struggles and broke free of the restraining device used to separate the head from the body.

Rate of water loss was measured at intervals of two to three hours from about 1000 to 0000 hours. All weighings were made on a Mettler balance to the nearest 0.1 mg. Minimum rates of water loss usually occurred during the evening. Occasional measurements made between 0000 and 1000 hours showed that the rate of water loss during this period was either the same as, or slightly higher than, levels set during the evening: if minimum values occurred at times of the day other than the evening, this is mentioned in the results. Animals weighing less than 50 g were put in 500 cc screwtop pickle jars; larger animals were put into a 5000 cc Agee screwtop preserving jar. The smaller jars were airtight; the larger container was sealed with wax. The rate of airflow used in the smaller containers was 150 - 200 cc/minute, for the larger 280 - 400 cc/minute.

If water is lost at the rate of 10 mg/hr into dry air flowing at 150 cc/minute, the resulting relative humidity of the air will be 4.3%. In the small chambers the highest rate of water loss used in the statistical treatment of the results was 11.5 mg/hr and the lowest 0.8 mg/hr; the difference in saturation deficit would lead to a systematic error of up to 4% in measured rate of water loss. In the large chamber the highest rate of water loss used was 25.0 mg/hr and the lowest 14.0 mg/hr, and in view of the higher airflow used in this chamber the relative humidity would never be as low as in the smaller chambers and not more than 0.5% higher; no allowance was made in the results for these errors. There was no detectable difference in values obtained until air flow rates fell to less than half the minimum flow rates usually adhered to: this happened on a few occasions if a tube servicing another animal chamber became disconnected. This suggests that under the experimental conditions used water loss in Egernia is limited by the rate at which water passes through the skin and not by the rate at which water vapour is removed from the outside of the skin by the airflow (Claussen, 1967).

Lizards were acclimated for at least two weeks at 27 C on a photoperiod of 12 hours light and 12 hours dark. With the exception of a higher humidity during the acclimation period, these conditions were the same as those prevailing during measurement of rate of water loss. Animals were given food and water ad lib until three days before the start of a measurement, when food was withdrawn. It was hoped that this period of acclimation, usually considered sufficient in reptilian studies (Ballinger and Schrank, 1970), would allow acclimation of metabolic rate to the same temperature and so avoid an elevated or depressed respiratory water loss in some animals (Dawson and Bartholomew, 1956; Harclerode and DeNicola, 1969). Those animals acclimated for longer than two weeks did not differ consistently from those acclimated for two weeks. The animals were acclimated to the temperature at which the rate of water loss was measured to avoid possible inter- and intraspecific differences in rate of acclimation of metabolism. 27 C was chosen owing to conflicting demands on the constant temperature room used to acclimate the animals.

While this technique does not differentiate between evaporative and excretory water losses, it was observed that, as would be expected, any large, transient increase in the rate of water loss was a consequence of excretion. Excretory water losses were very small in relation to the overall evaporative water loss. This would, however, be in part a consequence of the animals being unfed and unwatered during the experiment.

3.2.2 Statistical analysis of results.

The rate of water loss of an animal was taken to be the minimum measurement obtained up to four to five days after the basal level had been reached (see S3.3.2 for definition of basal level). The body weight of an animal was taken to be its body weight at the beginning of the experiment. Since the rate of water loss of an animal was not directly proportional to its body weight, the regression of water loss on body weight was calculated for each of the populations studied. To obtain a linear regression the results were transformed into logarithms before statistical analysis: water loss into log water loss (mg/hr), body weight into log body weight (g). After a preliminary test to determine whether or not the variances were homogeneous (they were), the regressions of the different populations and species were tested by analysis of covariance (ancova) to see if they differed either in intercept (adjusted mean) or slope. It was shown that there were no significant differences among the slopes but that there were significant differences among the adjusted means. The differences among the adjusted means were tested for significance by the sequential method described in Snedecor (1961, p 253 and p 402). The 5% and 1% percentage points used in these tests were taken from Snedecor (1961) and May (1952) respectively. The regressions, the Bartlett's test for homogeneity of variance, and the ancova were calculated according to Snedecor (1961).

Only the populations from which two or more individuals were sampled were treated statistically. Thus the single _E. m. margaretae_, the single _E. m. personata_ from Telowie Gorge and the single _E. multiscutata_ from Port Lincoln were excluded. This left 16 populations in seven species.

In the test for homogeneity of variance, data were used only for populations from which animals of a wide weight range were tested. This was to ensure that reasonably accurate estimates were made of the regression coefficients, and hence of the residual variances about the regression lines. Three of the 16 populations were thus excluded from this analysis, these being the American River and Wedge Island populations of _E. whitei_, and the Italowie Gorge population of E. m. personata. All 16 populations were used in the subsequent stages of the ancova.

In testing all possible combinations of the adjusted means of 16 populations taken two at a time, 120 tests are involved. If all the populations were the same, chance would result in some of them being judged significantly different on the basis of the samples compared (a Type I error). Conversely, there would be cases where two populations which differed would be judged as being the same on the basis of the samples compared (a Type II error). The sequential method of testing for differences among adjusted means is conservative in that it minimises the risk of committing a Type I error. This security is of course gained at the expense of an increased probability that Type II errors have been committed.

3.3 RESULTS

Examples of serial measurements of rate of water loss are presented in Figure 12. The rate of water loss was found to have a diurnal rhythm, the daily minima usually occurring during the evening. There was a progressive decline of values obtained on successive evenings. The decline in minimum evening values had two components: an initial, rapid fall occurring for less than ten days, and, in at least some species, a gradual fall which continued indefinitely.

3.3.1 Rapid decline in rate of water loss.

To illustrate the rapid decline graphically, the minimum evening value was noted for each day in experiments which were run long enough for minimum values to be about the same for at least four days. The time taken to reach the end of the rapid decline varied with the species, being 4 - 5 days for E. multiscutata and 8 - 10 days for E. kintorei. For each individual the minimum evening value for each day was expressed as a percentage of the lowest evening value obtained during the whole experiment. For all individuals of one species the mean of the percentages was calculated day by day; examples are shown in Figures 13 - 14. The rapid falloff reduced the minimum evening value by about 3% per day, and terminated in 10 days or less.

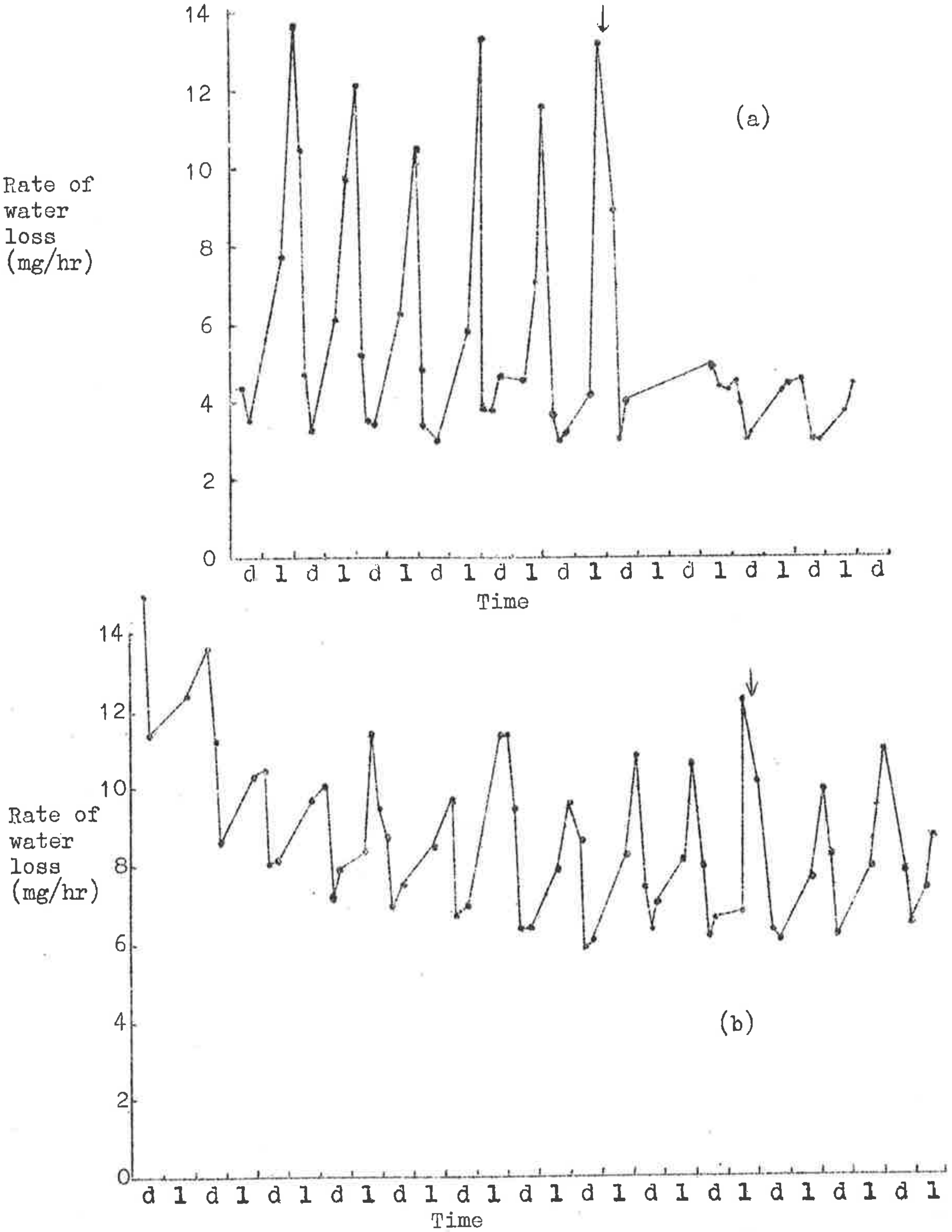


Figure 12. Examples of serial measurement of rate of evaporative water loss. (a) is an *E. multiscutata* from Marion Bay, initial weight 5.88 g, run for 10 days. (b) is an *E. m. personata* from Port Germein Gorge, initial weight 19.33 g, run for 13 days. "l" = light, "d" = dark. The arrows indicate rehydration during the experiment.

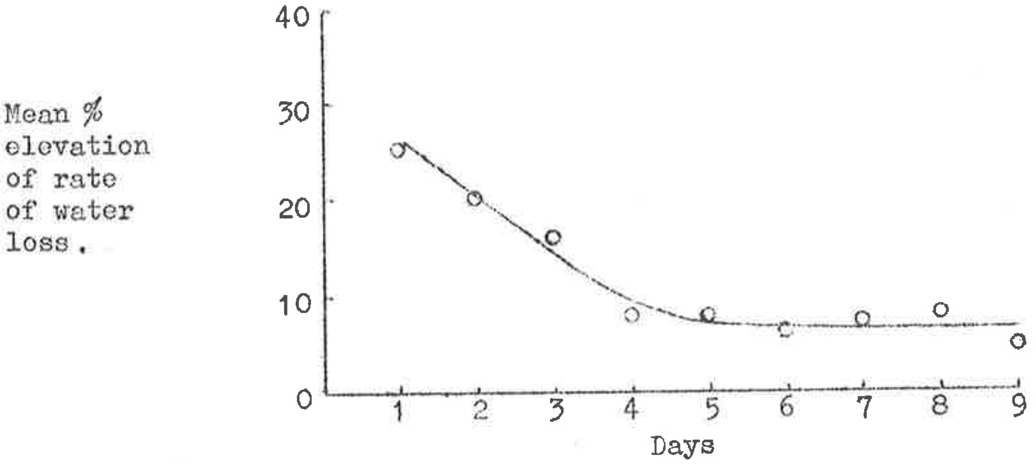


Figure 13. Decline in minimum evening values of rate of water loss in Egernia whitei at the beginning of an experiment. The basal level was reached in about five days. Line fitted by eye.

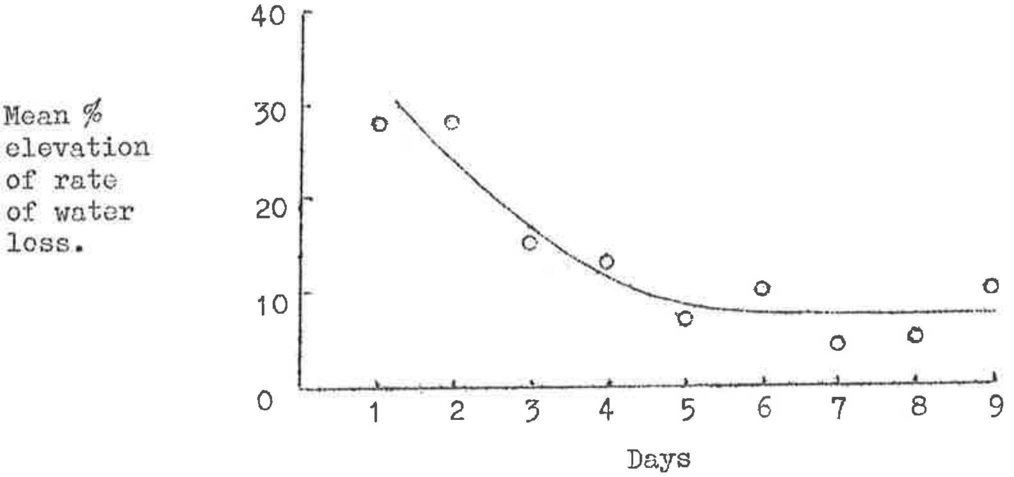


Figure 14. Decline in minimum evening values of rate of water loss in Egernia inornata at the beginning of an experiment. The basal level was reached in about five or six days. Line fitted by eye.

3.3.2 Gradual decline in rate of water loss.

In *E. whitei*, *E. margaretae*, *E. multiscutata* and *E. kintorei* some individuals were run for at least 20 days and up to 60 days, the animals usually being rehydrated at least once during the experiment. Once the rapid decline had terminated, the minimum evening values tended to decline slowly, by about 4% every 10 days. The minimum values obtained during this period of gradual decline are termed the basal level.

3.3.3 Origin of decline in rate of water loss.

The rapid and gradual declines in rate of water loss are so different in magnitude as to indicate that they have different origins. The rapid decline in rate of water loss would appear to be related to one or more of the following variables

(i) progressive dehydration,
(ii) progressive starvation,
(iii) acclimation to the new surroundings.

Dehydration can be virtually eliminated as an influence since in a number of experiments animals which had reached a basal level were rehydrated to the pre-experimental level. Although this produced an increase above the basal rate of water loss, this was slight in relation to the elevation above basal evident at the beginning of the experiment. Dehydration might contribute to the gradual decline in rate of water loss. Starvation can be virtually discounted as an influence since these lizards can survive for months without food and the decrease in metabolic mass during the first few days of the experiment would therefore be slight. One would also expect this variable to exert an influence declining only gradually with time; this was not the case. However, it is likely that the gradual decline in minimum values can be attributed in part to a declining metabolic mass. There is little direct evidence for a decline in activity as the animal acclimates to the experimental apparatus. Observations made while the lights were on indicated that activity declined during the first few days of the experiment. In some individuals the basal level was reached immediately, suggesting that these animals had been quiescent from the beginning. The observation that the rate of water loss usually remains high only for a few days at the beginning of an experiment is consistent with the acclimation hypothesis.

3.3.4 Experiments of short duration.

In a few of the earlier experiments measurements were continued for only three to four days, not long enough for the basal level to have been reached. In these short term experiments the value to which the measurements would have eventually fallen was estimated by reducing the minimum value obtained on each day of the experiment by the amount the observed value would be expected to be above the basal level. This amount was calculated by using whichever of the figures showing the rapid falloff in rate of water loss was appropriate for the animal being considered. For example, in the case of an *E. whitei* (see Figure 13), the observed minimum for day 1 was multiplied by 100/125, for day 2 by 100/120, and so on. The mean of the corrected values was taken to be the rate of water loss of the animal.

3.3.5 Reproducibility of replicates.

In *Egernia whitei*, *E. multiscutata* and *E. slateri*, replicate experiments performed on the same animal nearly always gave similar results. However, in *E. margaretae*, *E. inornata*, *E. striata* and *E. kintorei*, replicates sometimes gave differing values if the animals had been held in captivity for several months before they were tested. In an attempt to understand the origin of this variation, I measured the rate of water loss of an individual *E. m. personata* for 48 days, the animal being rehydrated a total of eight times during the experiment. The "basal level" obtained initially (about 10.6 mg/hr) was high but could be reduced to a stable value (about 4.7 mg/hr) by repetitive rehydration. The reduction in "basal level" was not progressive but via a series of stable levels, one stable level following another every time the animal was rehydrated. Thus the fully-hydrated animal possessed a number of different rates of water loss, suggesting that the phenomenon has a physiological basis. A stable basal level was reached after six rehydrations, and further rehydrations produced no further change in the basal level. It is possible that these successive declines in rate of water loss were related to thyroid function. Thyroid hypertrophy has been implicated in moulting in some species of lizard (Lynn, 1960), and the animal moulted early in this experiment. In many other experiments producing elevated values in *Egernia*, the animal moulted during the experiment. In other lizard species a hyperactive thyroid is correlated with an increased metabolic rate (Maher and Levedahl, 1959; Maher, 1964, 1965) and hence respiratory water loss. The effects of skin shedding on rate of water loss are transient (Benedict, 1932; Gans *et al*., 1968) and would not be related to an elevation of water loss extending over this period. Other hormones affect moulting and could also be involved in the elevation of rate of water loss e.g., injection of adrenocorticotrophic hormone (ACTH) has been shown to increase the interval between moults in *Anolis carolinensis*, and its mode of action is believed to be independent of thyroid hormones (Chiu and Lynn, 1970), but the relevance of these observations to the situation in *Egernia* cannot be determined without additional information. If the pars distalis of the pituitary of the toad, *Bufo bufo*, is inactivated or extirpated, shedding of the slough is inhibited, but keratinisation of the epidermis is not. This eventually results in the skin becoming thickly cornified (Jörgensen and Larsen, 1960). Jörgensen and Larsen inactivated the pars distalis of toads either by transplanting it into one of the eye muscles or by extirpating the median eminence, and found that injection of lysine vasopressin produced sloughing. Since injection of lysine vasopressin into toads from which the pars distalis had been removed did not produce sloughing, the authors suggested that vasopressin stimulated the release of a sloughing factor from the pars distalis, and that this sloughing factor might have been ACTH. It is possible that in those species of *Egernia* where replicate measurements of rate of water loss gave differing values ACTH secretion is reduced after prolonged captivity, and that the increase in circulating vasopressin levels when the animal is dehydrated during a water loss experiment stimulated ACTH secretion and hence moulting. However, it appeared that the frequency of moulting in E. inornata from Renmark which had been in captivity for several months was high regardless of whether or not the animals were dehydrated. It appears that prolonged captivity alters the hormonal state of the animal in some species, although just how is not evident at present.

In many other individuals where the basal level was high initially it could be reduced by rehydration. This reduction in rate of water loss by rehydration could only rarely be produced in species where replicates nearly always gave similar results (see S3.3.6 and S3.3.8, especially Tables 4 and 6).

The elevation of basal level appearing in some species of the Egernia whitei species-group seems only to occur in animals which have been kept for long periods in the laboratory (see S3.3.7 and S3.3.9), and is apparently independent of the procedure described in S3.2.1 used to acclimate the animals. I therefore regarded the elevated values as spurious and did not use them in the statistical analysis of results. In the animals for which it was possible that all of the replicates were influenced by prolonged captivity I used the lowest of the replicates obtained for each individual. In E. m. personata (see S3.3.7) I used all the results from the animals from Port Germein Gorge, Middle Gorge and Italowie Gorge, but only the lowest of the replicates of the animals from Wilpena. In E. inornata (see S3.3.9) I used only the results from animals which showed no sign of elevation of their basal levels (i.e., all the results of the animals from Alice Springs and Kyancutta, and the results of the animals from Renmark run soon after capture). In E. striata and E. kintorei (see S3.3.11 and S3.3.12) I used the lowest of the replicates. The procedure of using the lowest of the replicates introduces a bias into the results, since the more times an animal is run, the greater is the chance of obtaining a still slightly lower result. To counterbalance this, however, is the possibility that even the lowest of the replicates obtained was still elevated as a result of the effects of prolonged captivity. I used the lowest of the replicates in E. m. personata from Wilpena, in E. striata and E. kintorei. In general, where replicates were performed on other animals, the chance that the values were influenced by the period the animals had been in captivity was slight, and the mean of all the replicates performed on an animal was used in the statistical analysis. The mean used was the mean of the logarithms of the respective water losses and body weights of the replicates. The exceptions to this generalisation were two E. multiscutata described in S3.3.8.

3.3.6 Rate of water loss of Egernia whitei.

Thirty specimens were tested, from Remarkable Rocks (18 animals), American River (4), Black Mountain (6) and Wedge Island (2).

The rate of water loss reached a basal level in four to five days (see Figure 13); since four animals were run for four days, their values were adjusted to allow for this. All other animals were run for at least six days. Minimum values usually occurred during the evening, but were within 5% of the minimum evening value if they occurred at other times of the day.

The results are shown in Figure 15; replicates gave similar results and intrapopulation variability was comparatively small. Moulting had no effect on rate of water loss apart from a transient increase lasting about one day. Five animals were rehydrated during the experiment; in four there were small percentage changes in rate of water loss but in the fifth there was a larger percentage decrease (see Table 4).

Table 4. Basal rates of water loss in five E. whitei before and after rehydration.

Population	Before drinking mg/hr	After drinking mg/hr	% change in rate of water loss
Remarkable Rocks	2.62	2.73	+ 4
Wedge Island	5.44	5.34	- 2
Black Mountain	8.42	9.20	+ 9
Black Mountain	7.37	6.97	- 5
Black Mountain	4.31	3.41	- 21

Animals from Wedge Island had a significantly lower rate of water loss than any of the other populations (see Tables 10 and 11, S3.3.13). There were no significant differences within any other pairs of populations.

3.3.7 Rate of water loss of *Egernia margaretae*.

Nineteen specimens of *E. m. personata* were tested, from Telowie Gorge (1 animal), Port Germein Gorge (6), Middle Gorge (5), Wilpena (4) and Italowie Gorge (3). One specimen of *E. m. margaretae* from Reedy Creek Rockhole was tested.

E. m. personata. The rate of water loss took up to six days to reach a basal level. With the exception of two animals from Wilpena (run for four and six days respectively) animals were run for eight days or more. Minimum values were always obtained during the evening.

The results are shown in Figure 16. The animals from Port Germein Gorge, Middle Gorge and Italowie Gorge were run within three months of capture and variability within each population was comparatively small. There was little change in rate of water loss following rehydration in these animals (see Table 5).

Table 5. Basal rates of water loss before and after rehydration in four *E. m. personata* run soon after collection. Experiments continued at least five days after drinking.

Population	Before drinking mg/hr	After drinking mg/hr	% change in rate of water loss
Port Germein Gorge	5.92	5.69	- 4
Port Germein Gorge	5.97	6.01	+ 1
Port Germein Gorge	7.04	6.75	- 4
Italowie Gorge	5.23	5.06	- 3

The animals from Wilpena were run after being kept more than eight months in the laboratory and there was considerable variation between replicates. The regression line for this population was calculated from the runs giving the lowest value for each individual. It is possible that the rate of water loss of animals from Wilpena has been slightly overestimated. The experiment giving the lower value for the Telowie Gorge animal lasted 48 days and has already been described (see S3.3.5). The "basal" level of water loss of this animal fell during the first six rehydrations from a high of 10.6 mg/hr to 4.71 mg/hr on the 31st day. The subsequent lowest value was 4.46 mg/hr, and during the remaining time of the run the animal was rehydrated twice more. The value graphed for this animal from the 48 day run was 5.40 mg/hr and was obtained by extrapolating the line drawn through the basal level between days 31 - 48 to day 8. The Telowie Gorge animal was not included in the statistical treatment of the results. The rate of water loss of the Italowie Gorge sample was lower than the other samples, but the difference was not statistically significant (see Tables 10 and 11, S3.3.13).

E. m. margaretae. Five runs were performed on the one animal. The basal level was reached in about five days, and the daily minima occurred during the evenings.

The results are shown in Figure 16. The lowest of the five values lies as much below the values of the Port Germein Gorge E. m. personata as do the Italowie Gorge E. m. personata, and it seems that E. m. margaretae and Italowie Gorge E. m. personata have the same rate of water loss. The result obtained for the single specimen of E. m. margaretae was not included in the ancova. In the calculation of the values shown in Table 11, S3.3.13, the lowest of the replicates was used.

3.3.8 Rate of water loss of Egernia multiscutata.

Sixteen animals were tested, from Remarkable Rocks (8 animals), near Port Lincoln (1), 6 km north east of Marion Bay (4) and St Francis Island (3).

The rate of water loss reached a basal level in about four days, and all animals were run at the basal level for at least three days. Minimum values usually occurred during the evening; in one case the minimum was recorded during the early afternoon.

The results are shown in Figure 17. Replicates, which were performed on eight animals, usually produced similar results. In two cases replicates gave differing values. The animal from St Francis Island was rehydrated during the run giving an elevated value, but no change in rate of water loss resulted (see Table 6); this animal moulted during the experiment. In both the animals where replicates differed markedly the lower of the values was used in the ancova. It can be seen that the relationship between size and rate of water loss in the small animal from Remarkable Rocks was the same as the population as a whole.

Intrapopulation variability was comparatively small, and rehydration during an experiment had no large effect on rate of water loss - see Table 6.

Table 6. Basal rates of water loss in five *E. multiscutata* before and after rehydration during an experiment. Measurements continued for at least three days after drinking.

Population	Before drinking mg/hr	After drinking mg/hr	% change in rate of water loss
Remarkable Rocks	6.90	7.07	+ 2
Remarkable Rocks	2.96	2.96	0
Marion Bay	2.96	2.91	- 2
Marion Bay	2.57	2.49	- 3
St Francis Is (5.64 g)	3.36	3.43	+ 2

The populations from Remarkable Rocks and Marion Bay have the same rate of water loss; the animal from Port Lincoln (which was not included in the ancova) falls in the upper part of the range of variability of these two populations. The St Francis Island sample has a significantly lower rate of water loss than any of the other populations (see Tables 10 and 11, S3.3.13).

3.3.9 Rate of water loss of *Egernia inornata*.

Seventeen animals were used, three from 50 km south of Alice Springs, ten from Renmark and four from 25 km SSW of Kyancutta. From Figure 14 it can be seen that the basal level was reached in about six days; this resulted in the adjustment of the minimum value of one of the animals from Renmark (which was run for three days) from 3.05 to 2.75 mg/hr. All other specimens were run for at least eight days. The minimum values were always obtained during the evenings.

The results are shown in Figure 18. All of the animals from Alice Springs and Kyancutta, and five of the animals from Renmark, were tested within three months of capture; all produced results falling within a fairly narrow range. Two of the Alice Springs animals were tested again about six months after capture and, allowing for the increase in weight, the results agreed with the earlier measurements. Another five animals from Renmark were tested after being in captivity for at least three months, and there was a tendency for rate of water loss to increase with time spent in captivity. These elevated values could not be reduced by rehydration during an experiment. This elevation of rate of water loss was correlated with an increased frequency of moulting: none of the animals moulted during the ten experiments producing low values, but five moulted during the eleven experiments producing elevated values.

It would appear that the only results from Renmark animals in normal condition were the five obtained soon after capture, and only these five were included in the ancova. These results suggest that Renmark E. inornata have a slightly higher rate of water loss than Alice Springs animals, although the difference was not statistically significant (see Tables 10 and 11, S3.3.13).

The animals from Kyancutta were collected and tested shortly before submission of this thesis, and the results obtained were used to test some of the hypotheses formulated in the Discussion (see S3.4.2). Kyancutta E. inornata were not included in the ancova, but had a water loss - body weight relationship similar to E. inornata from other areas (see Figure 18).

3.3.10 Rate of water loss of Egernia slateri.

Five animals from 3 km south of Alice Springs were used. The basal level was reached after about six days and four animals were tested for at least seven days; the fifth was run for four days and this animal's value was adjusted to allow for this. The minimum value was usually obtained during the evening; occasionally it occurred during the morning or night but in such cases was never more than 10% below the minimum evening value.

The results are shown in Figure 19. Replicates were performed on two animals and agreed well.

3.3.11 Rate of water loss of *Egernia striata*.

Eight animals collected from Chilla Well were used. All trials were continued until a basal rate of water loss was reached, this usually taking about seven days. Minimum values usually occurred during the evenings; if they occurred at other times of the day they were within 5% of the minimum evening value.

The results are shown in Figure 20; replicates failed to give reproducible results. Two animals with apparently "elevated" basal rates of water loss were given water during an experiment; this reduced their basal rates of water loss (see Table 7). Rehydration failed to reduce the basal rate of water loss of a third animal which was "normal" (see Table 7). The "elevated" basal rates shown in Table 7 are not plotted in Figure 20.

Table 7. Basal rates of water loss of three *E. striata* before and after rehydration during an experiment. Only the "elevated" basal rates were reduced.

Body weight (g)	Whether or not basal level elevated before rehydration.	Before drinking (mg/hr)	After drinking (mg/hr)	% change in rate of water loss
23.0	elevated	9.22	6.52	- 29
31.9	elevated	15.00	6.77	- 55
31.9	not elevated	7.92	8.33	+ 5

3.3.12 Rate of water loss of *Egernia kintorei*.

Seven animals from 30 km south of Aileron were used. The basal rate of water loss was not reached for about ten days, and all measurements were made over at least this period. The minimum value was frequently obtained between 0000 and 1200 hours; these values were never more than 5% below the minimum evening value.

The results are shown in Figure 21. Replicates were performed on three animals and sometimes were not comparable. In all runs where elevated values were produced, the animal moulted shortly before, during or at the end of the experiment. In the two cases tested, rehydration had no effect on one elevated basal level but reduced the other (see Table 8).

Table 8. Basal rates of water loss before and after drinking in two *E. kintorei*. In both cases the basal levels before drinking were elevated.

Body weight (g)	Before drinking mg/hr	After drinking mg/hr	% change in rate of water loss
95.0	26.0	14.0 (a)	- 46
78.1	25.7	26.2 (b)	+ 2

(a) Once the "expected" basal level was reached, subsequent rehydrations did not further reduce rate of water loss.
(b) In a replicate experiment, when this animal weighed 62.8 g, its rate of water loss was 13.0 mg/hr.

Measurements were frequently continued for up to 20 days if an animal was rehydrated during an experiment. It was thought that starvation might produce a reduction in oxygen consumption (Belkin, 1965) and hence respiratory water loss (see also S3.3.2). In two individuals measurements were conducted for 30 days beyond the time required for the basal level to be reached. The basal rate of water loss fell by about 4% every 10 days, and as it was thought that this reduction would not have a significant effect on the results, no correction was made. In the two animals run for more than 30 days,

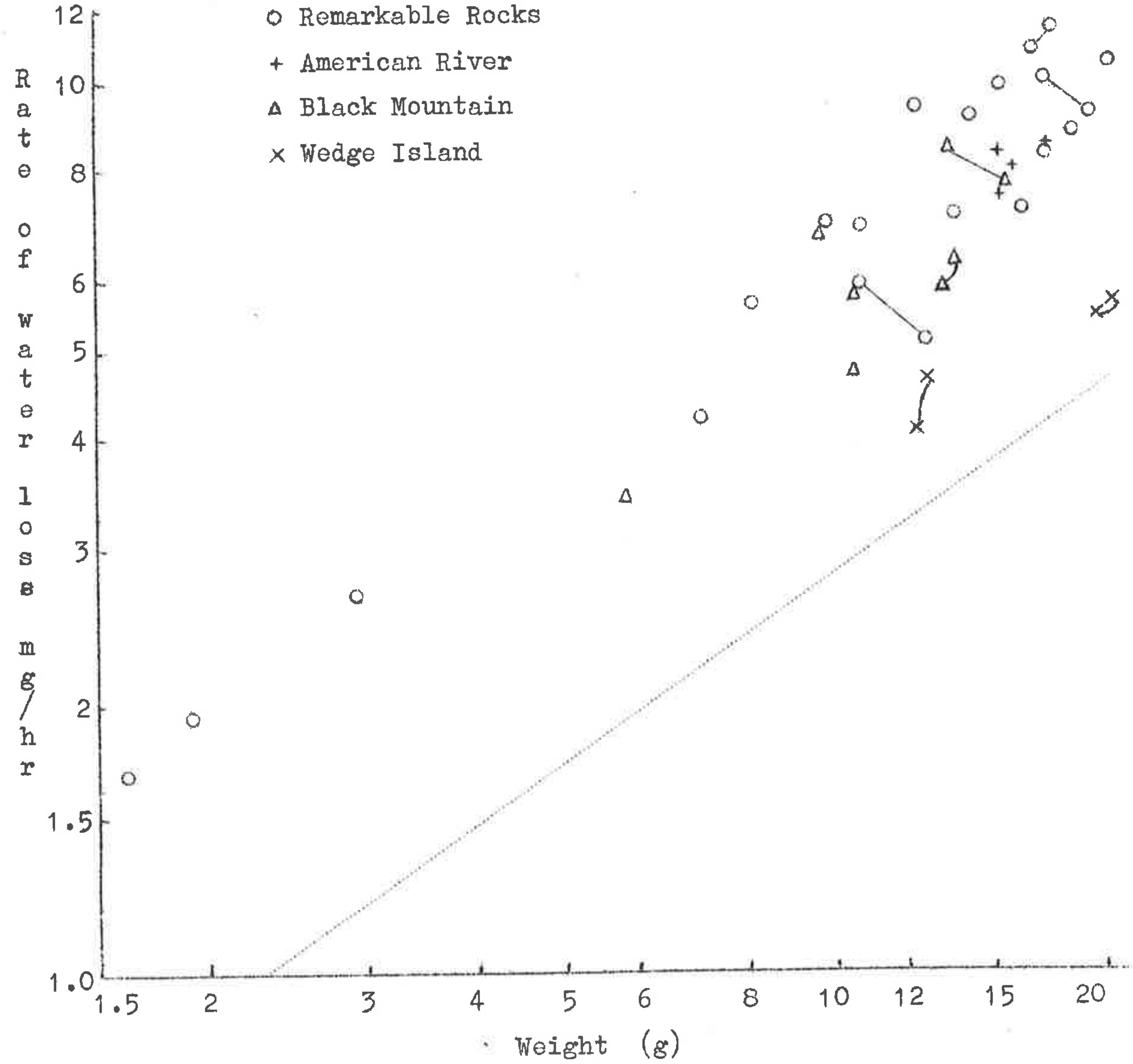


Figure 15. Basal rates of evaporative water loss of Egernia whitei from four areas. Replicates are connected by lines. The dotted line has a gradient of 0.70 and passes through the point (weight = 20 g, water loss = 4.6 mg/hr).

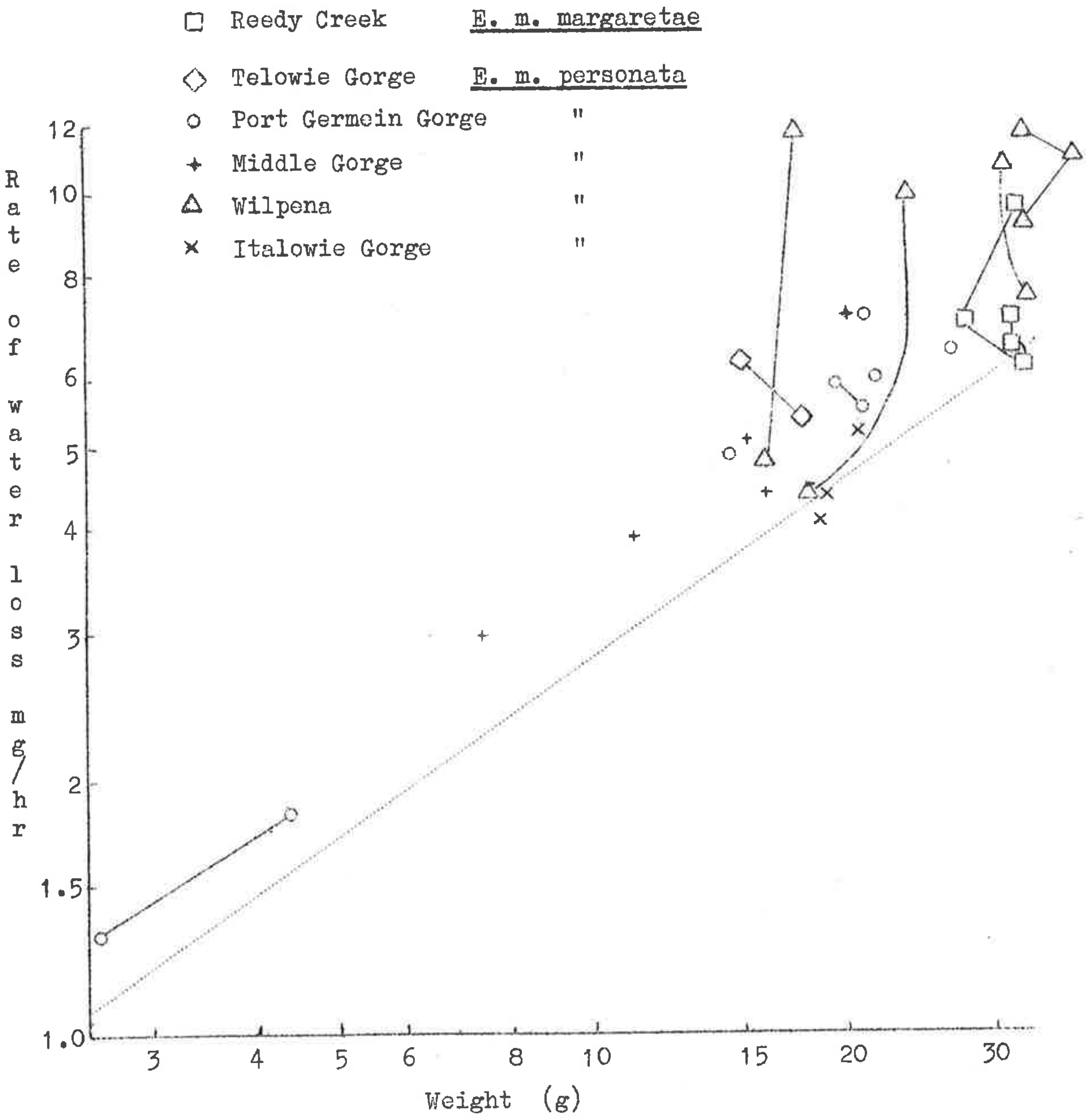


Figure 16. Basal rates of evaporative water loss of *Egernia margaretae* from six areas. Replicates are connected by lines. The dotted line has a gradient of 0.70 and passes through the point (weight = 20 g, water loss = 4.6 mg/hr).

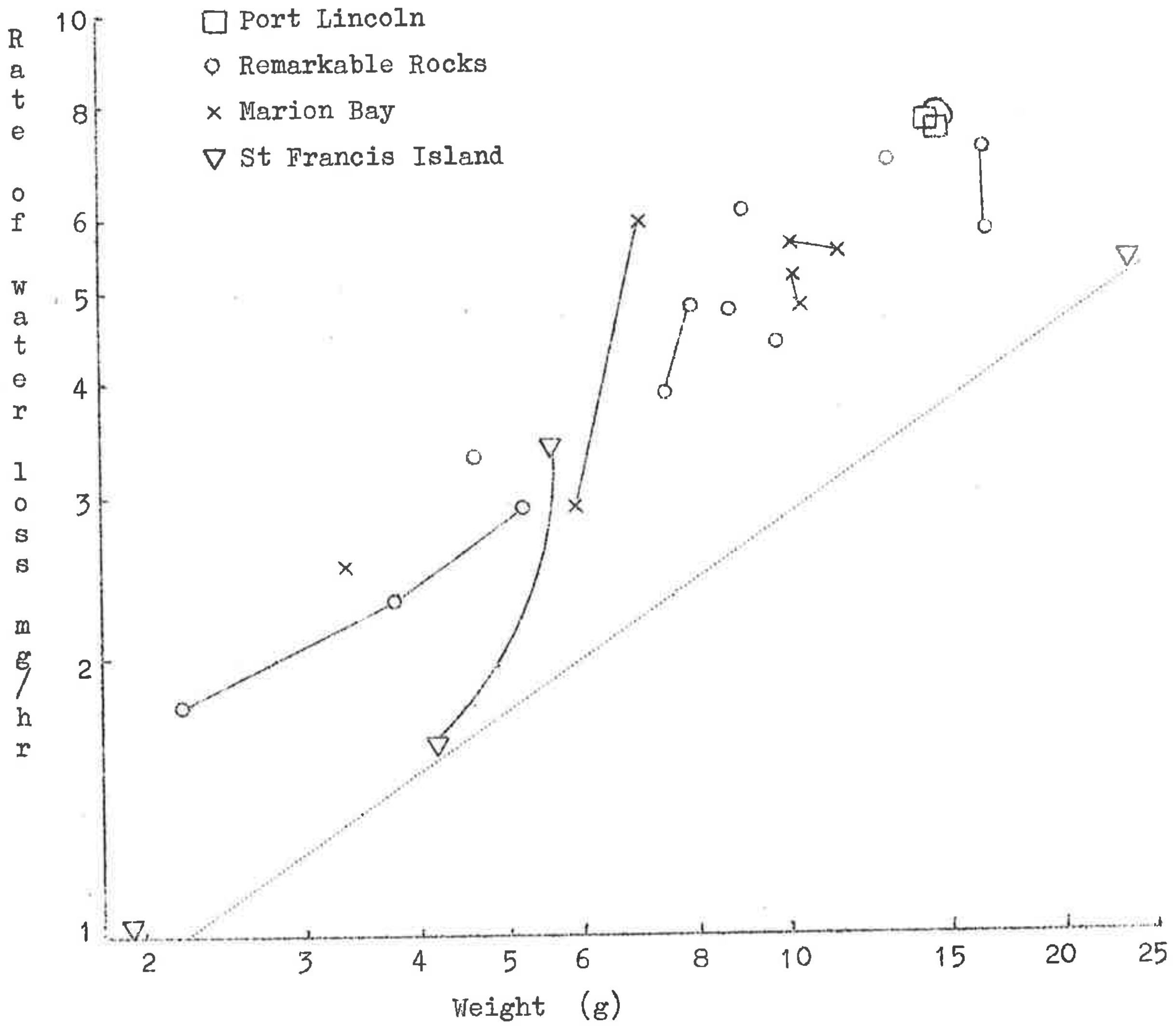


Figure 17. Basal rates of evaporative water loss of <u>Egernia multiscutata</u> from four areas. Replicates are connected by lines. The dotted line has a gradient of 0.70 and passes through the point (weight = 20 g, water loss = 4.6 mg/hr).

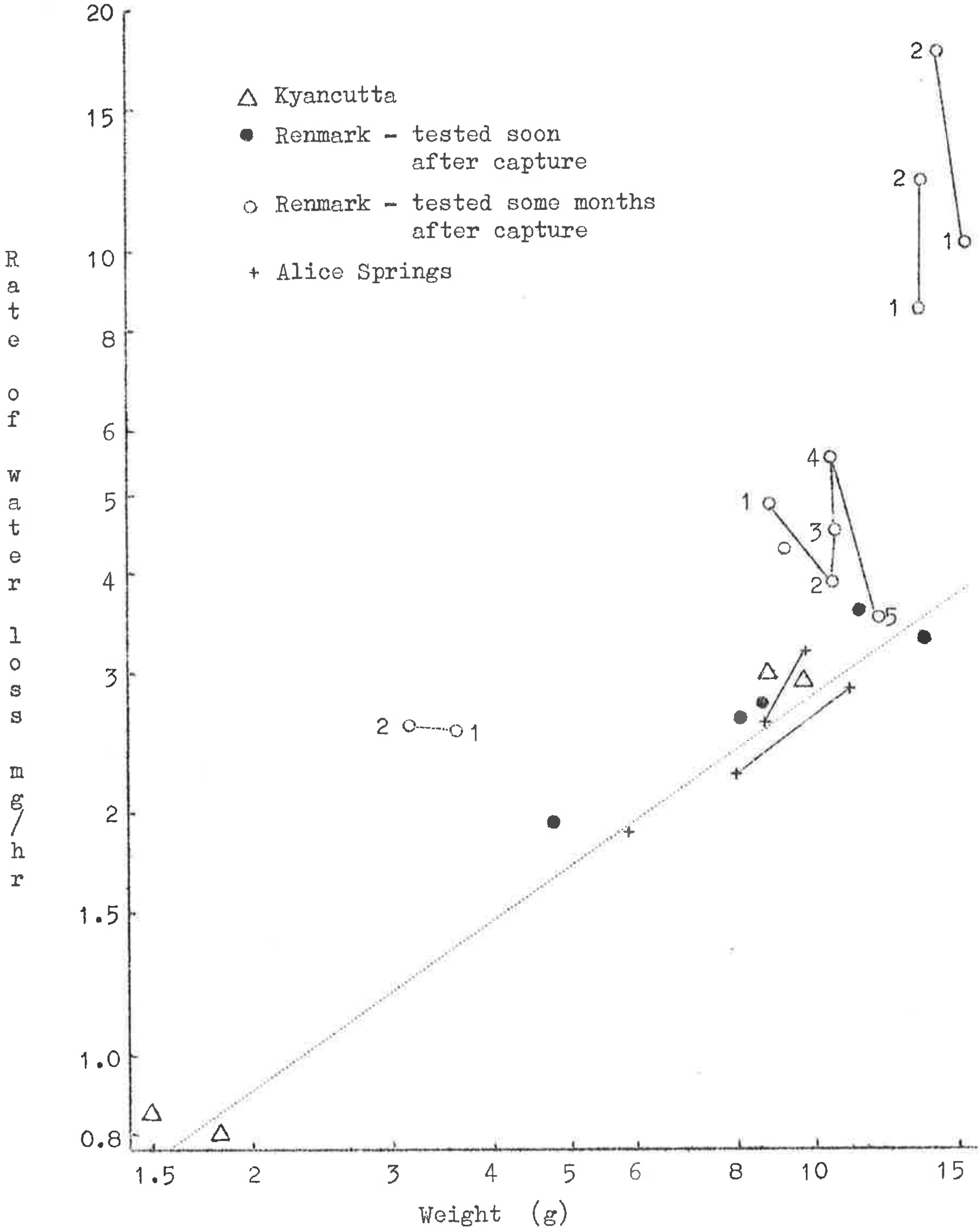


Figure 18. Basal rates of evaporative water loss of Egernia inornata from three areas. Replicates are connected by lines, and the numbering adjacent to the points indicates which experiment was performed first, second, etc. in the sequence of experiments. The dotted line has a gradient of 0.70 and passes through the point (weight = 20 g, water loss = 4.6 mg/hr).

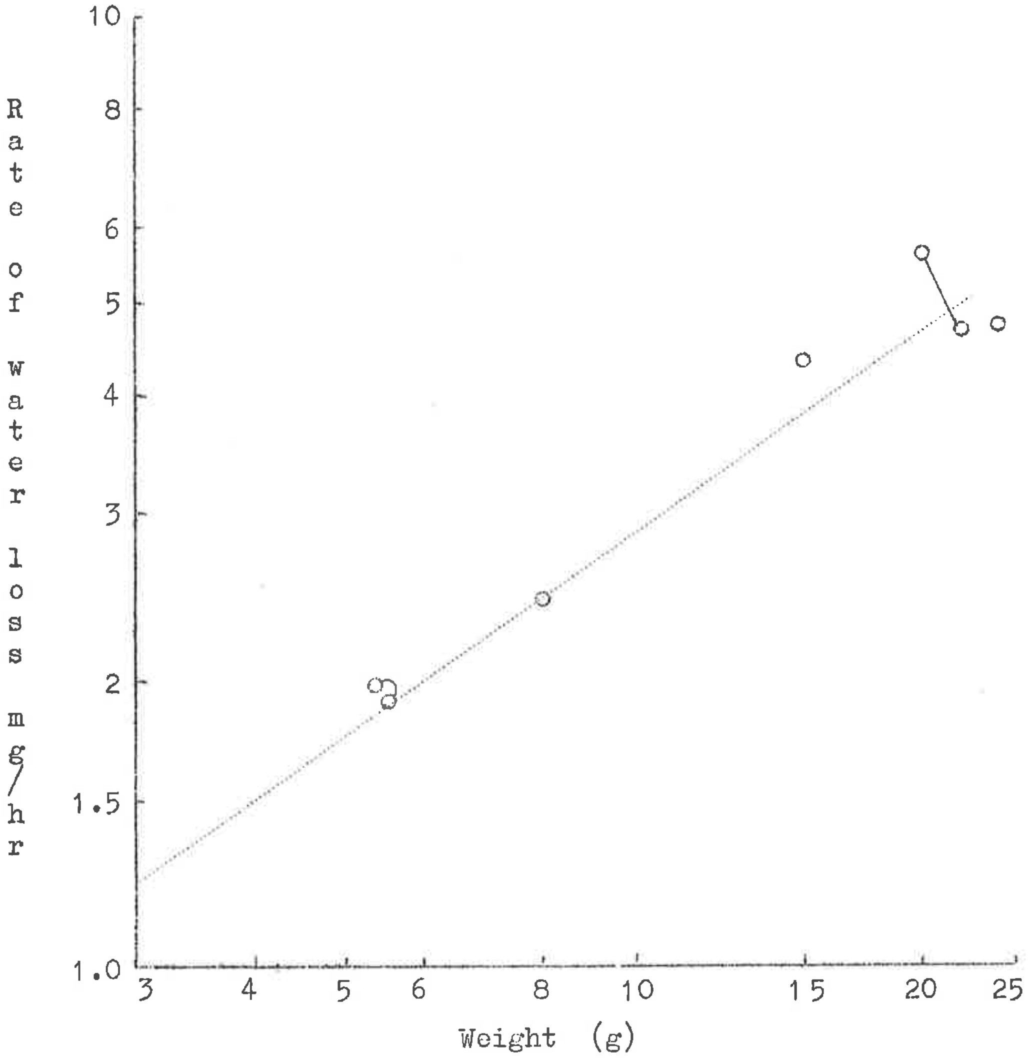


Figure 19. Basal rates of evaporative water loss of Egernia slateri from Alice Springs. Replicates are connected by lines. The dotted line has a gradient of 0.70 and passes through the point (weight = 20 g, water loss = 4.6 mg/hr).

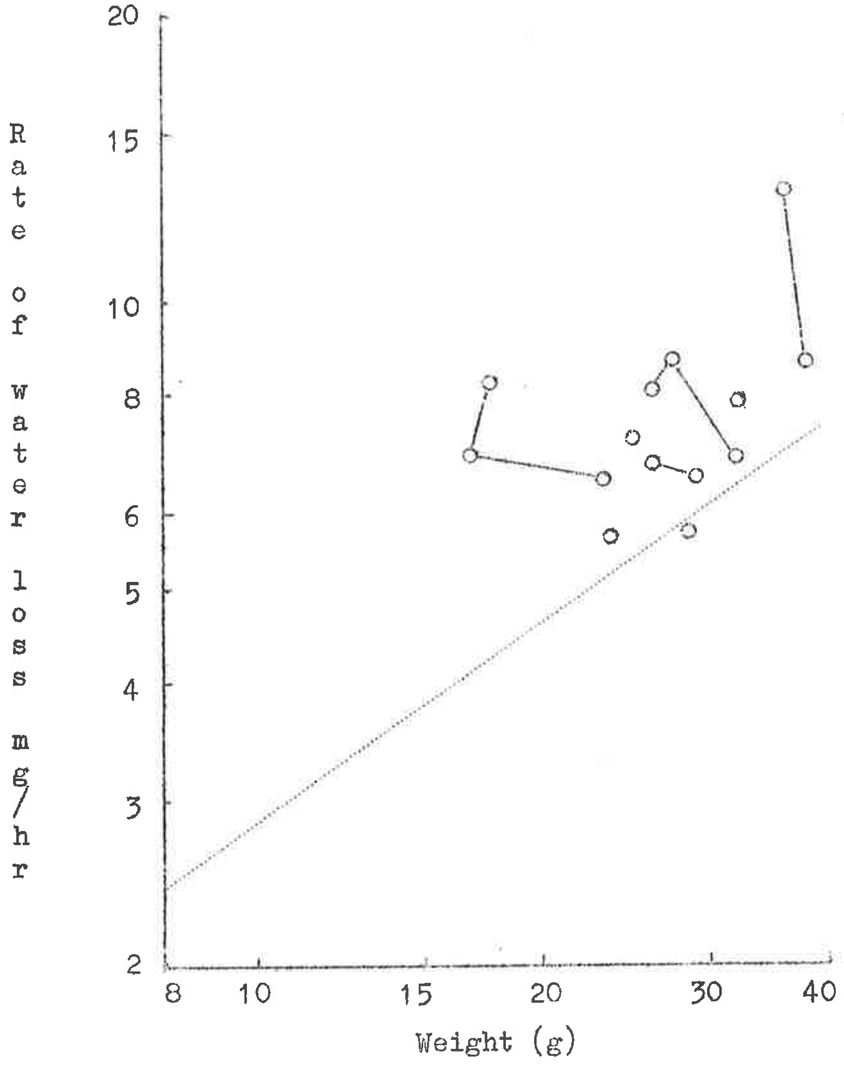


Figure 20. Basal rates of evaporative water loss of *Egernia striata* from Chilla Well. Replicates are connected by lines. The dotted line has a gradient of 0.70 and passes through the point (weight = 20 g, water loss = 4.6 mg/hr).

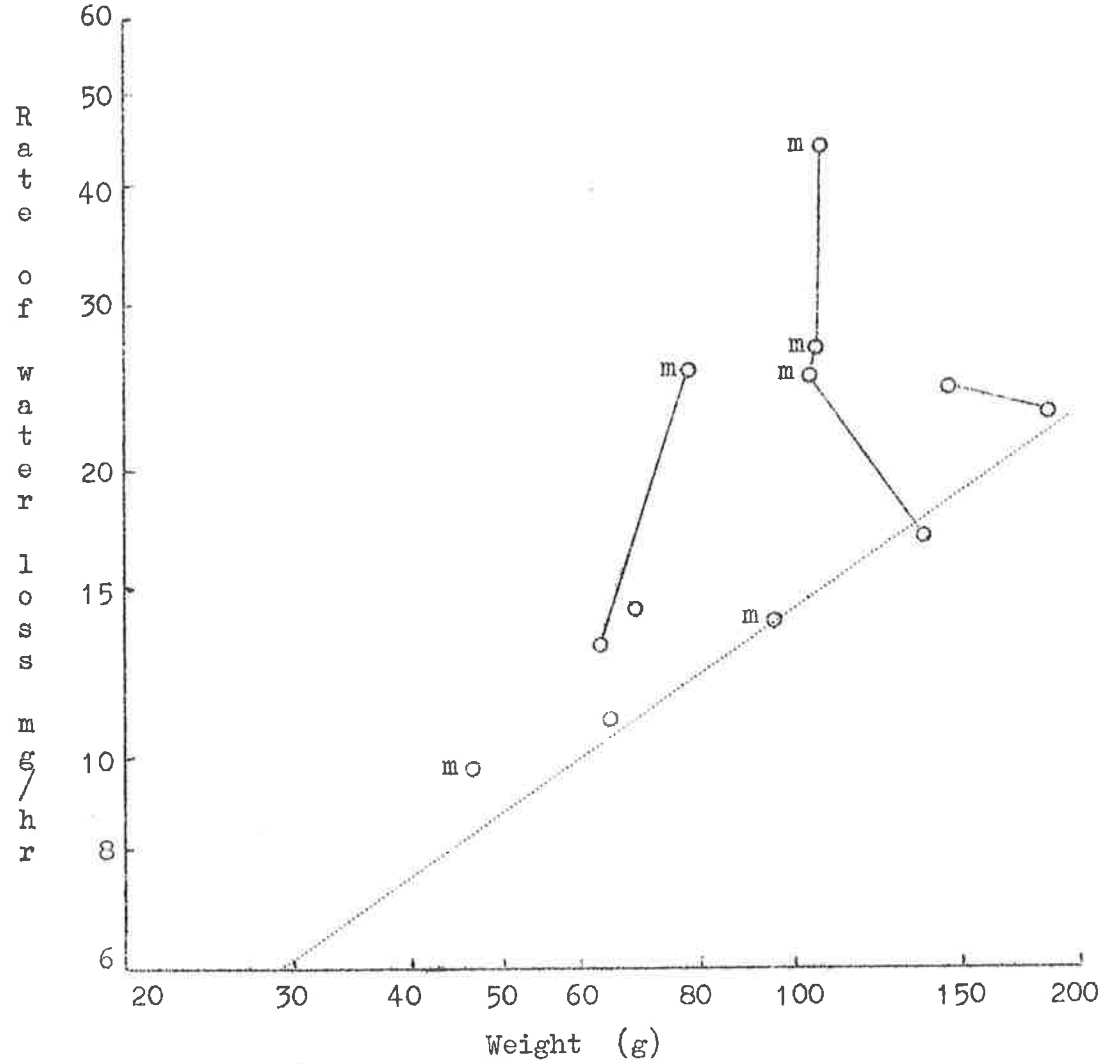


Figure 21. Basal rates of evaporative water loss of <u>Egernia kintorei</u> from Aileron. Replicates are connected by lines. "m" next to a point indicates that the animal moulted during or at the end of the measurement. The dotted line has a gradient of 0.70 and passes through the point (weight = 20 g, water loss = 4.6 mg/hr).

the values plotted in Figure 20 were obtained within four days of the basal level being reached.

3.3.13 Statistical treatment of results.

The variances about the regression lines were shown to be homogeneous, and the Chi-square value obtained is shown in Table 9.

The ancova used results from 91 animals, these being E. whitei from Remarkable Rocks (18 animals), American River (4), Black Mountain (6) and Wedge Island (2); E. m. personata from Port Germein Gorge (6), Middle Gorge (5), Wilpena (4) and Italowie Gorge (3); E. multiscutata from Remarkable Rocks (8), Marion Bay (4) and St Francis Island (3); E. inornata from Renmark (5) and Alice Springs (3); E. slateri (5); E. striata (8) and E. kintorei (7). The ancova showed that there were no significant differences in slope among the regression lines of the different populations and species (see Table 9), and the mean gradient was shown to be 0.70 (i.e., rate of water loss varies with $[\text{body weight}]^{0.70}$). However, there were shown to be highly significant differences among the adjusted means (see Table 9). The adjusted means, adjusted to a body weight of 20 g, are shown in Column 4, Table 11 (where they are expressed as mg/g.hr; the statistical tests were performed on the data transformed into log mg/hr). The results of testing for significance of the differences among the adjusted means taken two at a time are shown in Table 10. In E. whitei and E. multiscutata there were significant differences within each species between the population with the highest rate of water loss and the population with the lowest rate of water loss, and also between other pairs of populations (see Table 10 for levels of significance and Table 11 Column 4 for adjusted means). There were no significant differences between the populations of the temperate and semiarid zone species (E. whitei, E. m. personata and E. multiscutata) with the lowest rates of water loss per unit body weight and any of the arid zone species (the other four species; see Table 2), and there were no significant differences among the arid zone species themselves. It is possible that some Type II errors have been committed owing to low sample sizes (see also S3.2.2). Thus the non-significant difference between the Wedge Island population of *E. whitei* and the samples of the arid zone species might, if fact, reflect real differences between the populations from which the samples were drawn, and the non-significant differences among the samples of *E. m. personata* might reflect real differences among the populations.

Table 9. Summary of test for homogeneity of variance, and of the ancova testing for significance of differences among gradients and adjusted means of the log body weight - log water loss regressions of the *Egernia whitei* species-group.

Homogeneity of variance:

Chi-square with 12 d.f. = 6.45. Not significant ($0.9 > p > 0.75$)

Differences among gradients and adjusted means:

Source of variation	d.f.	Sum of squares	Mean square
Within	60	0.1902	0.003170
Regr. coeff.	15	0.01450	0.0009667
Common	75	0.2047	0.002729
Adj. means	15	1.3397	0.08931
Total	90	1.5444	

Test for differences among gradients:

$$F\,(15,\ 60) = \frac{0.0009667}{0.003170} = 0.305$$ Not significant

Test for differences among adjusted means:

$$F\,(15,\ 75) = \frac{0.08931}{0.002729} = 32.73$$ Highly significant, $p < 0.001$

Table 10. Significance of the differences between the adjusted means of the water loss - body weight regressions of the populations and species in the Egernia whitei species-group. Abbreviations are explained below the body of the table. See Table 11, Column 4, for the adjusted means (in mg/g.hr).

		E. whitei				E. m. personata				E. multi-scutata			E. in-ornata		sl	st	ki
		RR	AR	BM	WI	PG	MG	W	IG	RR	MA	SF	RE	AS			
E. kintorei		S	S	S						S	S						
E. striata		S	S	S						S	S						
E. slateri		S	S	S						S	S						
E. in-ornata	AS	S	S	S						S	S						
	RE	S	S	S						S	S						
E. multi-scutata	SF	S	S	S						S	s						
	MA					s	s	s	S								
	RR					S	S	S	S								
E. m. pers-onata	IG	S	S	S													
	W	S	S	S													
	MG	S	S	S													
	PG	S	S	S													
E. whitei	WI	S	s	s													
	BM																
	AR																
	RR																

S indicates significance at the 1% level, s at the 5% level, a blank that the difference is not significant.

E. whitei RR = Remarkable Rocks AR = American River
BM = Black Mountain WI = Wedge Island
E. m. personata PG = Port Germein Gorge MG = Middle Gorge
W = Wilpena IG = Italowie Gorge
E. multiscutata RR = Remarkable Rocks MA = Marion Bay
SF = St Francis Island
E. inornata RE = Renmark AS = Alice Springs

sl = E. slateri

st = E. striata

ki = E. kintorei

S3.3.13

Table 11. Maximum observed size, rate of water loss per unit body weight of an animal of maximum size, rate of water loss per unit body weight of an animal weighing 20 g, the ratio of the rates of water loss per unit body weight of maximum sized animals and animals weighing 20 g, and the rate of water loss of an animal of maximum size in the *Egernia whitei* species-group. n = number of animals.

Column 1 Species and population	n	Col 2 Max size (g)	Col 3 Water loss (mg/g.hr) max size	Col 4 Water loss (mg/g.hr) 20 g	Col 5 Ratio col 3 / col 4	Col 6 Water loss (mg/hr) max size
E. whitei						
Remarkable Rks	18	20.5	0.51	0.51	1.00	10.4
American River	4	17.0	0.49	0.47	1.04	8.4
Black Mountain	6	16.0	0.48	0.45	1.07	7.7
Wedge Island	2	20.5?	0.29	0.29	1.00	5.9
E. m. margaretae						
Reedy Creek	1	32.0?	0.19	0.23	0.83	6.2
E. m. personata						
Pt Germein Gge	6	27.0	0.27	0.29	0.93	7.2
Middle Gorge	5	25.5	0.28	0.30	0.93	7.2
Wilpena	4	33.0	0.24	0.28	0.86	7.8
Italowie Gorge	3	20.5?	0.23	0.23	1.00	4.8
E. multiscutata						
Remarkable Rks	8	16.5	0.45	0.42	1.07	7.4
Marion Bay	4	12.0	0.47	0.40	1.17	5.6
St Francis Is	3	23.5	0.24	0.25	0.96	5.6
E. inornata						
Kyancutta	4	10.0?	0.31	0.25	1.24	3.1
Renmark	5	15.0	0.27	0.25	1.08	4.1
Alice Springs	3	12.0	0.27	0.23	1.17	3.2
E. slateri						
Alice Springs	5	24.0	0.23	0.24	0.96	5.4
E. striata						
Chilla Well	8	38.0	0.22	0.27	0.81	8.3
E. kintorei						
Aileron	7	180	0.14	0.26	0.54	24

? signifies that an insufficient number of adults was collected to be certain that animals near the largest size in the population would have been included.

3.3.14 Significance of the value of the exponent in the equation relating water loss to body weight.

In my study it was not possible to directly measure respiratory and cutaneous water loss (see S3.2.1), and the question arises as to whether it is possible to interpret the value of the exponent (0.70, see S3.3.13) in the equation relating water loss and body weight in terms of the relative contributions of respiratory and cutaneous water loss. Thus, if the values of the exponents relating surface area and oxygen consumption to body weight were known, it should be possible to calculate the relative contributions of the two sources of water loss to the total so long as the two exponents were not equal, and if the following assumptions were made
(i) respiratory water loss varies directly with oxygen consumption,
(ii) the permeability of the skin to water does not change with age,
(iii) skin from different parts of the body has the same permeability.
Neither of the exponents relating surface area or oxygen consumption to body weight are known in Egernia, but it might be possible to predict the likely values of these exponents either theoretically or from reference to the literature.

If there are no changes in the relative proportions of an object as it increases in size, the exponent relating surface area to weight is 0.67. However, juvenile Egernias have relatively long appendages compared to adults (Storr, 1968) and it might be expected that the exponent would be less than 0.67 in Egernia, although how much less is uncertain. Green (1969) found an exponent of 0.67 for the lizard Varanus gouldii, Claussen (1967) found exponents of 0.83 for the lizard Anolis carolinensis and 0.47 for the lizard Uta stansburiana, and Gans et al. (1968) found an exponent of 0.63 for the snake, Elaphe climacophora. These data show quite a degree of variation in the exponent.

Roberts (1968b), working with Uta stansburiana, obtained an exponent of 1.03 relating oxygen consumption to body weight in March and April, but at other times of the year the exponent was less than this (although, according to Roberts, it was less reliably determined than during March and April). Dawson and Bartholomew (1956) obtained exponents ranging from 0.47 - 0.68 for Uta stansburiana and Sceloporus occidentalis tested at a variety of temperatures. By combining data from a variety of species they obtained an exponent of 0.54. By combining data from a variety of crocodilian reptiles, Huggins, Hoff and Valentinuzzi (1971) obtained an overall exponent of 0.93. Similarly, Bartholomew and Tucker (1964) obtained an exponent of 0.82 for several species of varanid lizards, and an exponent of 0.62 if they included additional data taken from the literature. Galvao, Tarasantchi and Guertzenstein (1967) combined data from several species of snakes and obtained exponents of 1.09 for Boidae and 0.98 for Colubridae. However, as Schmidt-Nielsen (1964, p. 245) and Gans et al. (1968) have pointed out, the exponents obtained by lumping data from several species are not necessarily the same as the exponents within any one species. The wide range of the few values reported in the literature does not allow any precise predictions of what the exponent is likely to be in any one species of Egernia.The ranges of the exponents relating oxygen consumption and surface area to weight overlap considerably, and it is possible that in Egernia they might be approximately the same.

Wide variations in the ratio of respiratory to cutaneous water loss have been reported in the literature, with values ranging from about 70% (respiratory) - 30% (cutaneous) in lizards (Chew and Dammann, 1961; Dawson et al., 1966) to about 30 - 70 in lizards (Dawson et al., 1966) and 10 - 90 in snakes (Prange and Schmidt-Nielsen, 1969). Once again, the literature does not help resolve the problem of how much of the water loss is respiratory and how much cutaneous in Egernia.

In terms of water balance, the main significance of the value of the exponent in Egernia (0.70) is that large animals have a lower rate of water loss per unit body weight than small animals, but a much higher total water loss.

3.4 DISCUSSION

3.4.1 Consideration of technique.

Before the rates of water loss of a number of individuals, or species, are compared, the behavioural and physiological state of the animal must be assessed to ensure that different individuals are being measured under comparable or at least known conditions. Certain of the variables involved, or which might possibly be involved, are easily controlled: body temperature, photoperiod, thermal acclimation, digestive state and the relative humidity around the animal are determined quite simply by the investigator.

However, to ensure that the animal is responding in the same way to these conditions is a more complex task and in this study two techniques were developed towards this end, these being serial measurement over a number of days and rehydration during the experiment. These methods usually produced results from animals in a comparable physiological state, which had acclimated to the chamber, and were inactive, providing a means by which the potential of a number of species to lose water could be accurately compared. However, in some cases the results produced by these techniques were not reproducible (e.g., E. inornata from Renmark), and evidently much remains to be learnt concerning the relationships between the hormonal state of the animal and its rate of water loss. Uncritical acceptance of rate of water loss measurements can be misleading.

It is these latter biological variables which have been inadequately considered in much of the literature on reptilian rate of water loss. Bradshaw (1965) is the only other worker who appears to have discovered that captivity can alter the rate of water loss of an animal. Bradshaw found that rate of water loss measurements made on Amphibolurus minor increased with the length of time the animals had been kept in captivity. He does not say whether the increase in water loss was correlated with an increased frequency of moulting, or whether he tried rehydrating the animals during an experiment. Some other workers appeared to recognise the problem and avoided it by using animals collected soon after capture. It is, of course, possible that effects of this nature occur in relatively few reptiles. Most workers have been aware of the influence of activity on rate of water loss, although some appear to have ignored it. Minnich (1970a) attributed the high rates of water loss obtained for Dipsosaurus dorsalis by Templeton (1960) to animal activity, a factor which Templeton does not mention. Bentley (1959), Warburg (1965a, 1965b, 1966) and Prange and Schmidt-Nielsen (1969) do not consider the influence of activity on their results, and it is not possible for a reader of their papers to take the influence of activity into account in any way. Chew and Dammann (1961), Dawson and Templeton (1963), Claussen (1967) and Gans et al. (1968) all obtained minimum measurements but did not verify that their minima obtained on day one were the same as the minima occurring during the night or on following days. I found that measurements made during the first day were elevated whether measurements were made in the dark or light. It would appear that an appreciable amount of the variability in the results presented by Gans et al. (1968) derives from the activity of their animals. The authors, however, claim that the data they present were from animals which did not show "significant activity". They presented data to show that ten separate runs on a single, invariably inactive, animal gave very similar results, and they also presented a graph (their Figure 2) showing the influence of activity on rate of water loss in a series of consecutive measurements on one animal. However, the value they drew from Figure 2 and presented in their Table 1 (1.85 mg/g.hr) is clearly not the minimum shown in Figure 2 (0.9 mg/g.hr). Several values around 1.85 mg/g.hr were obtained from periods in which activity was recorded as occurring, while the value of 0.9 mg/g.hr was obtained from a single period in which no activity occurred. Their criterion of "significant activity" still allowed activity to make a contribution to total water loss at least as large as that made by metabolism and the skin when the animal was at rest. While this did not obscure the difference between their tropical and xeric groups of snakes, it might have obscured any differences within either of the two groups. Green (1969) appreciated the importance of testing for diurnal activity patterns and then measuring at times when the animal was inactive, but his measurements were conducted over only one day.

Where there is the possibility of different diurnal activity patterns having a marked influence on the results, the approach used by Cloudsley-Thompson (1965), Dawson et al. (1966) and Bradshaw (1965, 1970) is preferable. Cloudsley-Thompson measured the amount of water lost over 24 hours, thereby including one complete cycle of the diurnal activity pattern. He usually continued measuring until the animal had died, and Figure 5 in his paper shows that the rate of water loss declined progressively over a number of days in some of the animals he studied, while in others it remained constant. Dawson et al. measured rate of water loss on several occasions during the first 24 hours and then at times 24 hours apart after this. From the data presented in Figure 1 of their paper acclimation to the experimental apparatus occurred within six hours, rate of water loss remaining fairly constant after this. Bradshaw (1965, 1970) standardised the period of measurement to either 12 or 24 hours and in the case of 24 hours included one complete cycle of the diurnal activity pattern. As the results obtained by Dawson et al. and Bradshaw were then related to the aridity of the areas from which their animals were taken, they assumed that both the potential to lose water and the amount of activity exhibited by the animals under the experimental conditions used were representative of the animals' performances in the field. Although it can reasonably be expected that this assumption holds true in the case of the potential to lose water, no evidence was presented to show that this was the case with activity.

Warburg (1965a, 1965b, 1966) used measurement periods of less than 24 hours as well as 24 hours in some experiments but made no attempt to consider the contribution of activity to rate of water loss or the role of diurnal activity patterns in relation to the particular times at which he made his measurements.

It is possible that by using telemetry to monitor activity of animals kept in completely dark containers reliable minima could be obtained on the first night if the animals were completely inactive; none of the workers using data collected only over one 24 hour period has done this. In my work, although activity was not monitored, measurement of rate of water loss on the first night typically produced values 20 - 60% higher than the subsequent minimum, and measurement at 30 minute intervals revealed that water was nevertheless lost at a constant rate. This suggested that the effects of low activity were averaged out over a number of 30 minute measurement periods, or possibly that metabolism was increased owing to unfamiliarity with the new surroundings; whatever the explanation, values near the basal level usually did not occur during the first evening in Egernia.

3.4.2 Discussion of results.

A priori it would appear that an animal could reduce its rate of water loss per unit body weight either by getting bigger or by reducing its skin permeability and/or its respiratory water loss per unit body weight. However, an increase in size results in an increase in total water loss, even though water loss relative to body weight is reduced. The extent to which different populations and species have exploited these alternatives can be deduced from Table 11, S3.3.13. In order to compare the ability of animals to reduce their respiratory water loss per unit body weight and their skin permeability, the influence of body weight on the comparison must be eliminated, and, where necessary, all log water loss - log body weight regressions were mathematically extrapolated to an animal weight of 20g. The rate of water loss of a 20 g lizard is defined as the standard water loss for the purpose of comparing populations. Figures for the standard water losses of the various populations are presented in Column 4 of Table 11. The ratio of the rate of water loss per unit body weight of maximum sized animals to the rate of water loss per unit body weight of animals weighing 20 g reflects the influence of size on rate of water loss per unit body weight, and figures are given in Column 5, Table 11. The maximum size attained within a population was used to express the influence of size of adults on rate of water loss. The average size of breeding adults might be a preferable index, but is known with even less certainty than the maximum attained size.

In any one species where more than population was sampled, there was a tendency for rate of water loss (in mg/g.hr of adult animals; see Column 3, Table 11) to decrease in the arid parts of its range (see Tables 1 - 3 for climatic data). These decreases were due to a decrease in skin permeability and/or respiratory water loss per unit body weight, body size playing a minor role in determining the differences between populations within any one species (see Columns 4 and 5, Table 11).

However, when comparing rates of water loss of species it becomes apparent that significant water economies per unit body weight have been made by increasing body size - see especially the values for E. inornata and E. kintorei in Columns 3, 4 and 5, Table 11. But in order for an adult E. kintorei to effect a 50% reduction in rate of water loss per unit body weight compared to an adult E. inornata, the E. kintorei has to be 1100% larger and lose 800% the total amount of water.

There are a number of interesting features about the variation between and within species of the standard water losses, these being the similarity between the lowest standard water losses observed within the various species, the tendency for the highest standard water loss observed in any one species to be correlated with the aridity of the areas occupied by that species, and the tendency of most of the standard water losses of the different populations within any one species to be similar. However, before these features are documented in more detail, or interpreted, I will briefly describe the aridity of the most and least arid of the areas from which specimens of each of the species were collected in relation to the aridity of the most and least arid areas in which that species occurs. Climatic data for the collection localities are presented in Tables 1 and 3.

Considering the E. whitei habitats, it is not clear from climatic data that Wedge Island is more arid than Black Mountain, or vice versa (see S2.3.5). E. whitei probably occur in areas more arid than these two localities. They are recorded as occurring on

Yorke Peninsula (the peninsula on which Marion Bay is situated) (Storr, 1968), although the exact locality is unknown (Houston, pers. comm.). Generally speaking, Yorke Peninsula is more arid than Wedge Island. E. whitei occur in parts of Victoria which are appreciably more arid than Wedge Island. E. whitei occur in areas much less arid (e.g., Tasmania) than any of those from which I collected.

Italowie Gorge is in the most arid part of E. m. personata's range, and Port Germein Gorge, at the southern end of E. m. personata's distribution, is about the least arid area in which E. m. personata occur. From S2.2.4 it appeared that E. m. margaretae only survive within the arid zone in microhabitats which offer relief from aridity. The implication drawn was that E. m. margaretae have become extinct in more arid areas outside these microhabitats. Presumably there has also been strong selection for arid adaptation within the present areas of their occurrence.

E. multiscutata, like E. whitei, have a wide distribution and it is difficult to decide what are the most arid parts of their range. St Francis Island would certainly approach these arid areas in aridity. Remarkable Rocks is one of the least arid areas in which E. multiscutata occur.

The Simpson Desert is the most arid area where E. inornata occur but the area south of Alice Springs from which E. inornata were collected is only slightly less arid than this. Renmark is much less arid than Alice Springs, but E. inornata occur in areas less arid than Renmark (e.g., Kyancutta on Eyre Peninsula, and western Victoria).

E. slateri resemble E. m. margaretae in that they are found in only a few small localities in the arid zone offering relief from aridity. They have probably been strongly selected for arid adaptation in their present areas of occurrence (see S2.2.7 for observations on mortality among E. slateri during drought).

The population of E. striata studied is not from the most arid parts of this species' range: E. striata occur in areas receiving considerably less January rainfall than Chilla Well.

E. kintorei occur in areas possibly slightly more arid than

Aileron.

Examination of the lowest standard water losses from each species examined in the E. whitei species-group shows a variation of 0.23 - 0.29 mg/g.hr (see Table 12). It appears that populations of E. whitei and E. striata occur in areas more arid than those I collected from, and, if these two species are eliminated from the comparison, the variation is reduced to 0.23 - 0.26 mg/g.hr. None of these differences approach significance, and it seems that the limit below which the standard water loss cannot be reduced is about the same for all the species. Until the relative contributions of respiratory and cutaneous water loss are known for each of the various populations and species, no specific interpretation in terms of skin permeability of respiratory water loss can be made.

Table 12. Lowest standard water loss found in each species of the E. whitei species-group. Data from Table 11.

Species	Number of populations tested	Population with lowest standard water loss	Lowest standard water loss (mg/g.hr)
E. whitei	4	Wedge Island	0.29
E. m. personata	4	Italowie Gorge	0.23
E. m. margaretae	1	Reedy Creek	0.23
E. multiscutata	3	St Francis Is	0.25
E. inornata	2	Alice Springs	0.23
E. slateri	1	Alice Springs	0.24
E. striata	1	Chilla Well	0.27
E. kintorei	1	Aileron	0.26

In those species (excluding E. inornata: see S3.3.9) where three or more populations were sampled, examination of the standard water losses of populations from the less arid parts of their respective ranges shows that these are similar in each species (see Table 13). This similarity suggests that each species has an optimum

Table 13. Standard water losses of populations from the less arid parts of the ranges of the species from which three or more populations were sampled. *E. inornata* was excluded. Data from Table 11.

Species	*E. whitei*	*E. m. personata*	*E. multiscutata*
Standard water loss (mg/g.hr)	0.51	0.30	0.42
	0.47	0.29	0.40
	0.45	0.28	

level for its rate of water loss. The most plausible interpretation of the phenomenon is in terms of genetic homeostasis (Lerner, 1954; Mayr, 1963; Dobzhansky, 1970). Thus, within any one species, both genetic homeostasis and the aridity of the environment influence the genotype of a population, genetic homeostasis being dominant in the less arid parts of a species' range, and aridity dominant in the more arid parts. If, as appears likely, genetic homeostasis influences the standard water loss of most populations of a species, several conclusions follow, among them being:

(1) The optimum level would appear to reflect the level of aridity to which the species has been exposed through time. The levels of aridity of the habitats occupied by the species of the *E. whitei* species-group apparently depend largely on variables other than the optimum level of rate of water loss (e.g., behaviour, see S5.0), and the optimum level would appear to reflect the degree of arid adaptation of other parts of the animal's genotype.

(2) Since it is difficult to conceive of a selection pressure which would cause the optimal level of rate of water loss to increase, while prolonged aridity could cause it to decrease, it logically follows that if the optimum level changes at all it can only decrease. However, the difficulty of conceiving of an appropriate selection pressure does not mean that one does not exist, and although the above deduction has phylogenetic implications it is probably a too poorly substantiated line of evidence to pursue.

(3) Although *E. whitei* occur in areas considerably less arid than any of those from which I collected animals, animals from less arid

areas (e.g., Tasmania) would not be expected to have standard water losses much higher than the populations I studied. In the cases of *E. m. personata* and *E. multiscutata*, populations were sampled from about the least arid areas in which each of these species occurs.
(4) The lowest standard water loss observed in *E. whitei* was 0.29 mg/g.hr. Even though populations of *E. whitei* occur in areas which appear to be more arid than Wedge Island (see above) these populations might not have standard water losses much lower than 0.29 mg/g.hr. In experiments selecting for either an increase or a decrease in a certain character, the character changed only to a certain extent (Lerner, 1954; Mayr, 1963, p 285 - 289). Thereafter, a decline in fitness (e.g., due to sterility, or developmental abnormalities) resulted in stabilisation, despite continued selection and the presence of residual genetic variability. Similarly, it is possible that 0.29 mg/g.hr is the limit below which *E. whitei* cannot reduce their standard water loss. Consistent with this suggestion is the fact that of all the species examined, *E. whitei* shows the greatest absolute and percentage reductions in standard water loss in the more arid parts of its range compared to the less arid parts (0.51 - 0.29 = 0.22 mg/g.hr, a 43% reduction in the case of *E. whitei*, compared to 0.42 - 0.25 = 0.17 mg/g.hr, a 40% reduction in the case of *E. multiscutata*, and smaller reductions in the other species).

The tendency for the highest standard water loss in any one species to be correlated with the aridity of the climates of the areas occupied by that species can be seen in Table 14. The highest standard water loss found in a species would reflect the optimum level of that species. I can suggest no explanation for the pattern of the data in Table 14 other than that in the preceding discussion on genetic homeostasis and the optimum level.

E. inornata from about the most arid part of the species' range and from an area of lesser aridity have similar standard water losses (0.23 and 0.25 mg/g.hr). This suggests that in this species the optimum level is close to the lowest standard water loss observed in this species. This would also appear to be true of *E. striata*,

Table 14. Highest standard water losses observed in the species in the _Egernia whitei_ species-group from which more than one population was sampled in relation to the aridity of the species' habitat. Kyancutta _E. inornata_ excluded. Data from Tables 2 and 11.

Species	Range of habitats occupied	Number of populations sampled	Highest standard water loss (mg/g.hr)
E. whitei	Humid - subhumid	4	0.51
E. multiscutata	Subhumid - semiarid	3	0.42
E. m. personata	Semiarid	4	0.30
E. inornata	Arid	2	0.25

where the standard water loss of 0.27 mg/g.hr was found in a population which was not from the most arid part of this species' range. However, only a single population of _E. striata_ was studied, and the preceding statement presupposes that the lowest standard water loss occurring in _E. striata_ is 0.23 mg/g.hr. The same might also be true of _E. kintorei_, although no relevant data are available: the only population sampled was from the more arid parts of this species' range.

It is apparent that if the rate of water loss was measured of _Egernias_ taken randomly from the ranges of the different species, a pattern of decreasing water loss with increasing aridity of environment would be found, this being the pattern which has been recorded in the literature.

An opportunity to test some of the hypotheses presented in the preceding pages arose in April, 1972, when I collected four _E. inornata_ from Kyancutta. Kyancutta is one of the least arid areas in which _E. inornata_ occur. The standard water loss of Renmark _E. inornata_ was 0.25 mg/g.hr, and since Renmark is a less arid part of _E. inornata's_ range it was predicted that Kyancutta _E. inornata_ would have a standard water loss of about 0.25 mg/g.hr (cf., Table 13). Secondly, since the habitats occupied by _E. inornata_ are generally more arid than those of the other species listed in Table 14, it was predicted that the standard water loss of *E. inornata* would be less than 0.30 mg/g.hr (the lowest standard water loss of a species other than *E. inornata* listed in Table 14). The observed standard water loss of Kyancutta *E. inornata* was 0.25 mg/g.hr, a result which supports the hypotheses that there is an optimum level for the standard water loss in each species and that the value taken by the optimum level is correlated with the aridity of the species' habitat.

An unexplained phenomenon, and yet one which has apparently been of considerable significance to lizards of the *E. whitei* species-group (see S5.0), is that no population of any species has a standard water loss lower than 0.23 mg/g.hr, although in nearly all the species this value is equalled or closely approached. The phenomenon appears to be unrelated to the experiments referred to above (when discussing the lower limit to standard water loss in *E. whitei*) in which artificial selection was applied to populations in attempts to induce large phenotypic changes. In these experiments it was observed that the phenotype changed only to a certain extent. The optimum level in *E. inornata* is very close to the lower limit below which standard water loss apparently cannot be reduced, and this might also be true for the other widely distributed arid zone species. Assuming that the optimum levels for standard water loss observed in the *E. whitei* species-group result from genetic homeostasis, then since it appears that genetic homeostasis is dependent to some extent at least upon the presence of genetic heterozygosity (Lerner, 1954), one would clearly expect to be able to obtain some reduction in standard water loss in *E. inornata* without exhausting genetic variability. Also, since it appears that the phenotype can deviate to some extent from the level set by genetic homeostasis without a marked loss in fitness due to sterility or developmental abnormalities, one would expect to find standard water losses below the optimum level in the more arid parts of *E. inornata's* range. It would appear that some other factor prevents the species reducing their standard water losses below 0.23 mg/g.hr. Thus it is possible that while any further reduction in standard water loss (e.g., possibly by increasing skin thickness) would result in the animal's benefiting from a reduced rate of water loss, greater disadvantages might result from the interactions between the modification required to reduce rate of water loss and the animal's environment. Thus there could be a net loss of fitness. This crucial problem clearly requires further work before it can be solved.

3.4.3 Comparisons with other workers.

Roberts (1968a) controlled both the physical and the biological variables and produced results from inactive, chamber acclimated animals. She obtained a result for Uta stansburiana stejnegeri, a lizard inhabiting xeric areas, of 0.48 mg/g.hr at 27 C in dry air for animals weighing 2 - 5 g, a result slightly higher than arid zone Egernia species of the same weight.

Braysher (1972) obtained minimum measurements on chamber acclimated Amphibolurus maculosus. A. maculosus inhabit the dry surfaces of some of the salt lakes in arid northern South Australia. Animals weighing 11 g had rates of water loss of 0.18 mg/g.hr in dry air at 37 C. This is considerably lower than the lowest values (about 0.27 mg/g.hr) observed for any member of the Egernia whitei species-group of the same weight in dry air at a lower temperature (27 C).

Sexton and Heatwole (1968) monitored activity and measured rate of water loss of the tropical lizards Anolis limifrons and Anolis auratis until death. Their results, obtained during periods of inactivity, show that these two species have much higher rates of water loss than Egernia, even though their measurements were made at 21 C and 55% relative humidity. Unfortunately it was not stated whether there was any trend in the results obtained during periods of inactivity with length of time the animals had been desiccated or time of day.

Even though some workers using minimum measurements of rate of water loss measured over only one day, this might not have had an excessive influence on their results. Chew and Dammann (1961) obtained values at 27 C for Uma notata, Dipsosaurus dorsalis, Phrynosoma solare and Crotalus scutellatus which are about the same as those of the arid zone Egernia species reported here. The results obtained by Gans et al. (1968) for various species of snakes at 27 C are, in general, considerably higher than the results obtained for Egernia.

As might be expected from the differences in technique, the results obtained by Dawson et al. (1966), Cloudsley-Thompson (1965), Bradshaw (1970) and Warburg (1965a, 1965b, 1966) are much higher than the results obtained by the other workers referred to above, though Cloudsley-Thompson found that the rate of water loss of a gecko (Tarentola annularis), deprived of water and weighed at intervals of 24 hours, fell dramatically over a period of four months from about 1.5 mg/g.hr to about 0.04 mg/g.hr, during which time the animal lost over 50% of its body weight (its initial weight was 25.89 g, its final weight 12.82 g).

4.0 DIURNAL EXPOSURE PATTERNS AND THERMOREGULATION

4.1 INTRODUCTION

Diurnal exposure patterns and thermoregulation were studied to determine whether the interspecific differences in diurnal exposure pattern observed in the field are consequences of differing regional temperature regimes and/or of innate behavioural differences. If environmental temperature regimes control behaviour, the differences in daytime exposure observed in the field would result from radiant heat levels and ground surface and air temperatures being too high or too low during parts of the daytime for the animals to remain abroad in certain geographical areas. If innate behavioural differences control exposure, exposure patterns could differ because animals avoid exposure at certain times of the day regardless of temperature, or as a result of the selection of different environmental temperatures for emergence and retreat.

The approach was to compare the exposure patterns and thermoregulation of the different species under the same environmental conditions in the laboratory. Any inherent differences in either diurnal exposure patterns or thermoregulation should then become apparent.

Two climates were provided; in both the animals were supplied with a dark, relatively cool refuge. The first was a simulated day-night cycle in which air and ground temperatures were usually so high as to preclude continuous exposure during parts of the daytime. Heat levels were adequate for the preferred body temperature to be reached during the early part of the evening and at all times of the daylight hours other than dawn. This climate was designed to determine whether the species behaved similarly when they retreated to the refuge in the presence of high environmental temperatures, and whether the species differed in their tendency towards nocturnal exposure when temperatures during the daylight hours had been high. The second climate, using thermal gradients, permitted the animals to remain continuously exposed and the preferred body temperature to be reached at all times of the day but not the night. This regime was designed to determine whether any of the species voluntarily avoided exposure at times of the day when temperature conditions were suitable for exposure.

4.2 METHODS

4.2.1 Recording equipment.

In many of the experiments, exposure was recorded by a 16 mm camera supplied by W. Vinten Ltd, London. One frame of the six pens was taken from above every five minutes, illumination being supplied by a synchronised electronic flash. Neither the flash nor the noise made by the camera appeared to disturb the animals in any way. Ilford FP4 film was used in 10 m lengths, one length lasting about four days. The film was processed and any animal exposure detected by examination with a microscope.

Temperatures were recorded by using glass bead thermistors connected via appropriate electrical circuits to a recorder (a 5 mv, 12 channel recorder, model ER-30-34, supplied by Yokogawa Electrical Works, Ltd, Tokyo, Japan). Temperature could be read directly from the recorder chart over the range 10 - 40 C with a maximum error of 0.1 C; beyond this the response of the thermistor circuit became non-linear and calibration charts were used. Lizard body temperatures almost always fell within the 10 - 40 C range. The thermistors used were Mullard type VA 3000, P 3 K 3, 3.3 Kohms at 25 C and are cylinders about 1 mm in diameter and 3 mm long. The thermistors were connected to the recorder either by lengths of figure 8 twinflex, 2 mm by 1 mm outside dimensions, or by 1 m lengths of a flex made from two strands of 39 guage copper wire (0.13 mm diameter, covered with plastic) fed down a length of 0.8 mm outside by 0.5 mm inside diameter clear vinyl tube, this flex being connected to the recorder by the larger twinflex. The clear vinyl tube was supplied by Dural Plastics and Engineering Pty Ltd, Dural, New South Wales. Thermistors were either inserted into the animal's cloaca or positioned on the dorsal surface of the base of the tail, and were held in place with 1.25 cm wide strips of adhesive cloth tape. The thermistor leads were tied at a point 100 cm from the thermistor to lengths of nylon cord stretched from one side of the pen to the other. The cord was 60 cm above the ground. Although the leads became slightly twisted and tangled during the day, this did not appear to restrict the movement of the animals.

Owing to delays in purchasing the recorder and designing the thermistor circuits, the recorder was not available until half way through the project.

4.2.2 Experimental environments.

An air conditioned room in which temperature but not humidity could be controlled was used for the behavioural work. St Girons and St Girons (1956) concluded that humidity had little influence on exposure. Owing to its design, the cooling unit of the air conditioner was able to cycle a maximum of five times an hour, and this led to the temperature in the room varying by up to 7 C between cut out and cut in of the unit. Mean air temperatures over periods of one hour or so were, however, constant. The cycling of the air conditioner resulted in a much smaller cycling of the lizards' body temperatures; this effect was 0.3 C in 8 g animals and decreased as the size of the animal increased.

The room was disturbed by humans only during the night to service the recording apparatus, feed and water the animals etc. Disturbance during the daytime led to marked changes in exposure patterns.

The animal pens are shown in Figures 22 - 23. The size of the individual pens was 90 by 50 cm, and the partitions separating them were glass. No interactions between lizards in adjacent pens were observed. These pens were used in all the experiments.

The conditions of light and temperature at different times of the day in the various regimes used are summarised in Figure 24.

4.2.3 Thermal gradient regime.

4.2.3.1 Experimental conditions. The environment used in these experiments is illustrated in Figure 22. Dawn, daytime and dusk were crudely simulated by using red heat lamps to establish the thermal gradient during dawn and dusk, and white during the daytime

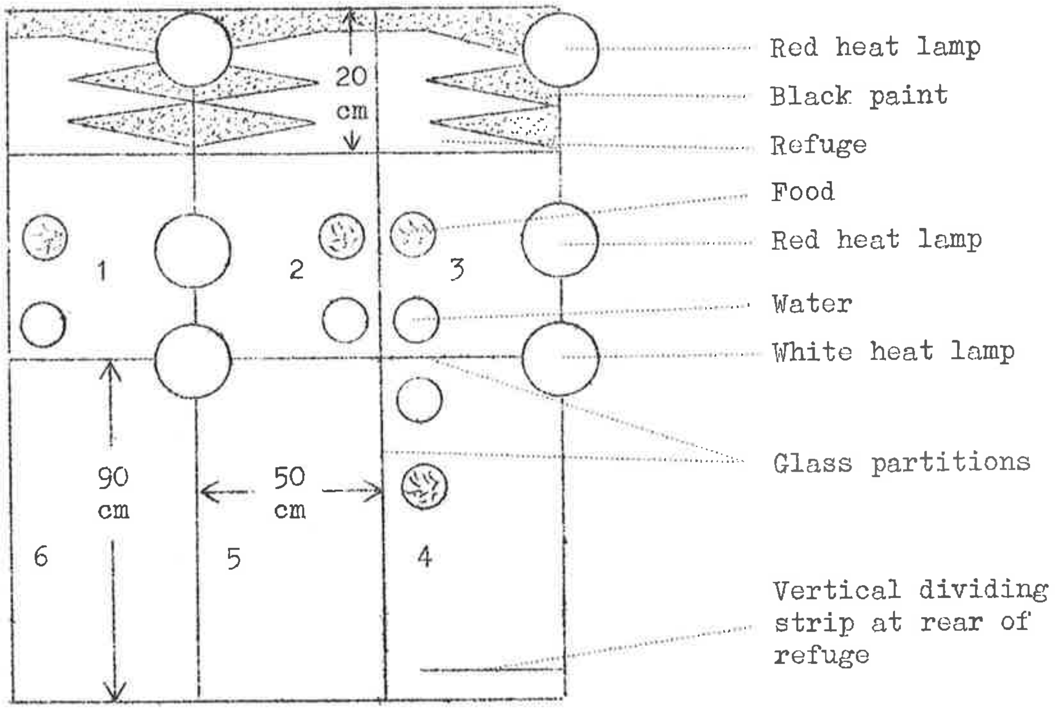


Figure 22. View from above of heat lamps, refuges, food and water in pens 1 – 3 during the experiments using the thermal gradient regime. To show the vertical dividing strip, pen 4 was drawn without the lamps or refuge. A lip at the front of the refuges prevented the animals climbing on top of them. The heat lamps above the refuges were switched on only when the animals were provided with thermal gradients within their refuges. Details for pens 5 – 6 are not shown. Dimensions as shown.

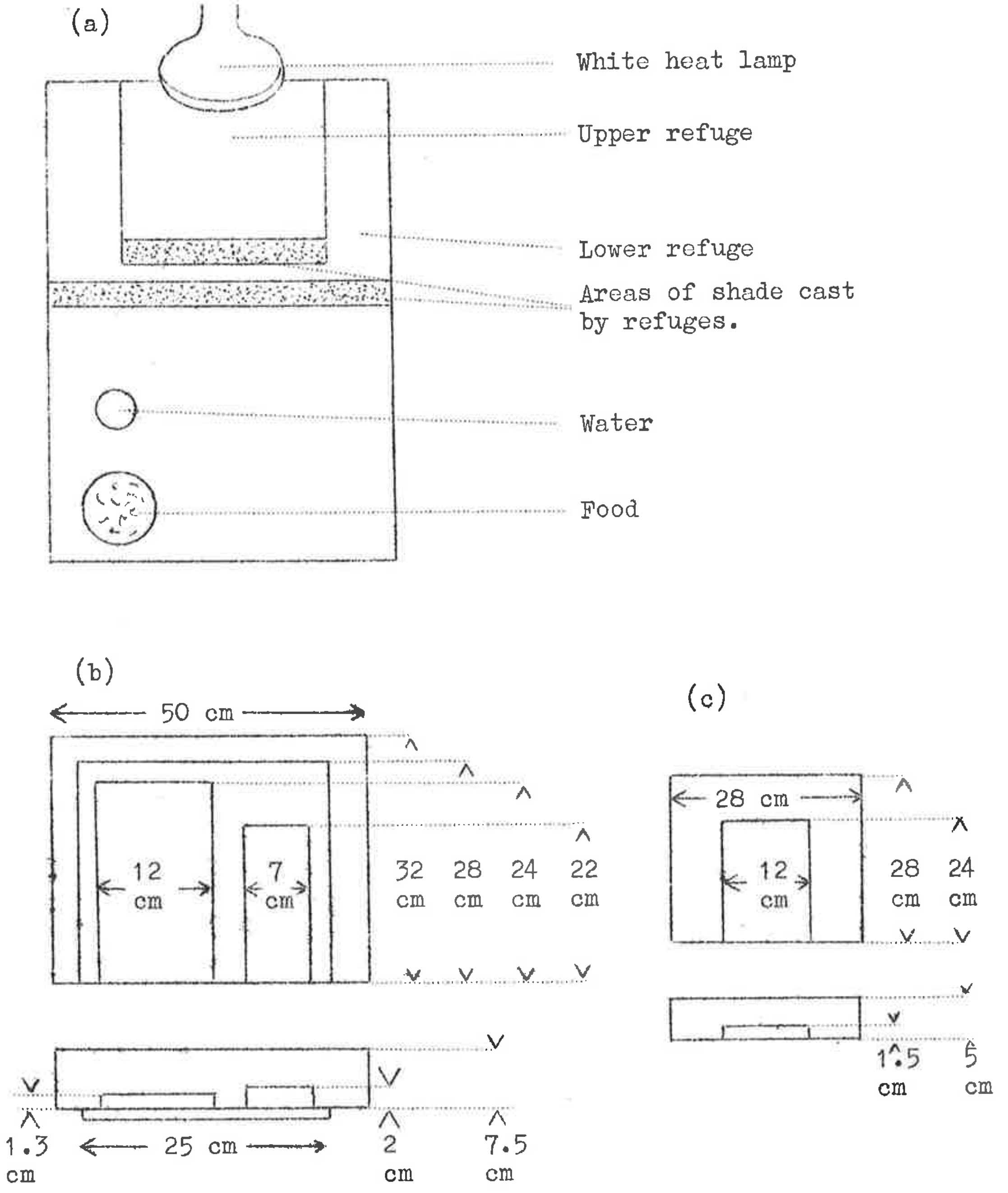
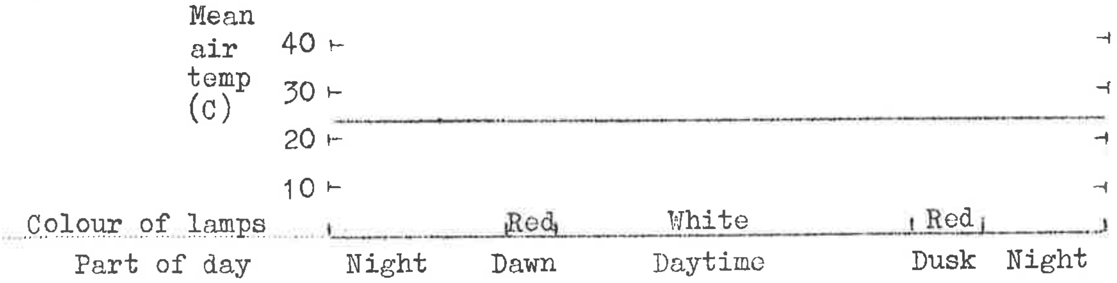
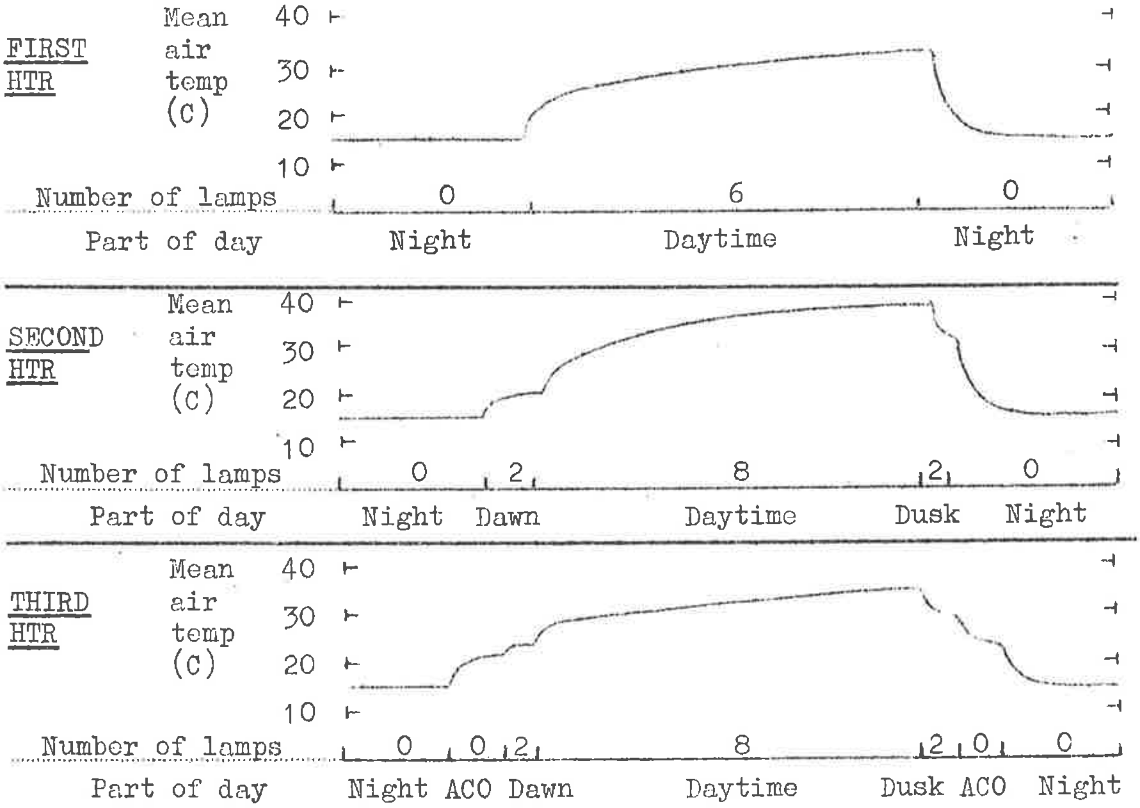


Figure 23. Environment used in high temperature regime experiments. (a) View from above of pen 1. The food and water shown were supplied as described in the text. (b) See through view from above and in front of the lower refuge and its base plate. Dimensions as shown. Note that cavities in refuges are not drawn to scale. (c) See through view from above and in front of the upper refuge. Dimensions as shown.



Thermal gradient regime. The red and white heat lamps switched on during the daylight hours provided sufficient heat for the animals to reach their preferred body temperatures outside their refuges. In nearly all of the experiments the refuges were at 24 C throughout the day.



"ACO" = air conditioner's cooling unit switched off.

High temperature regimes (HTR). The number of heat lamps indicated provided heat and light to all pens; all lamps were white. Air temperatures shown are approximate. Refuge temperatures varied - see S4.2.4.1. The three HTRs are shown.

Figure 24. Diurnal changes in temperature and lighting in the various experimental regimes.

(see Figure 24). All heat lamps were 250 watt, although the red ones produced less light than the white. During dawn, daytime and dusk, the range of temperatures continuously available to the animals outside their refuges was 24 C to over 50 C; during the bulk of the night, the only temperature available to the animals was 24 C. For several hours after dusk, the animals could elevate their body temperature above 24 C by positioning themselves on the warm patches of sand which had been the hottest parts of the thermal gradients during the daytime and dusk. A red heat lamp aimed away from the pens and left on during the night provided a low level of light to all pens.

The refuges were sheets of galvanised iron held above the ground surface by strips of wood; the height of the refuge above the ground varied with the size of the animal. The refuges were open at the front and enclosed at the sides and back; a vertical dividing strip parallel to the back of the pen gave the animals a confined space at the rear of the refuge. The floor of the refuge was made from plaster of Paris to stop the animals digging. The temperature in all parts of the refuge was 24 C. Occasionally red heat lamps placed above the refuges were used to establish thermal gradients within the refuges; the range of temperatures available to the animals within their refuges was then about 27 - 40 C.

Food and water were continuously available.

4.2.3.2 Measurement of diurnal exposure pattern. It was possible to determine whether or not an animal was exposed by a number of methods.

(i) Photography of the animal pens provided direct sightings of exposed animals. This method was unreliable during periods when an animal was directly beneath and obscured by one of the heat lamps. This occurred during the daytime if the animal was beneath the lamp which was not switched on, or more commonly during the evening if the animal was resting on the warm patch of sand beneath a heat lamp which had been switched off recently. Results produced by photography and occasional direct observation by myself established the reliability of the following method, which depends upon the animal's body temperature.

(iia) The animal was scored as being exposed if its body temperature was above 24 C and increasing or constant.

(iib) The animal was scored as being exposed if the fluctuations of its body temperature followed the cycling of the air conditioner. It was observed that the body temperature of an animal inside its refuge did not cycle in this manner. As examination of the photographic film was a time consuming process, the animal's body temperature was used to determine exposure patterns in most of the experiments. Since either retreat to the refuge or moving to a cool part of the photothermal gradient produced rapid falls in body temperature which could not be attributed to either one of these origins with certainty unless the fall in body temperature was large, an animal was judged as having moved inside its refuge only if its body temperature fell below 27 C and did not cycle with the air conditioner. 27 C most adequately differentiated between short term falls in body temperature occurring within the thermoregulatory pattern (these falls being of short duration, rarely reaching 27 C, and during which the animal might either retreat to its refuge or a cool part of the gradient) and those cases where the animal retired to its refuge for long periods (usually one hour or more), when its body temperature fell to below 27 C within 15 - 30 minutes. It was unusual for a fully hydrated animal to be outside its refuge at a body temperature below 27 C for longer than 30 minutes.

(iii) In some experiments the thermistor was taped onto the dorsal surface of the base of the tail. The temperature traces with regard to average thermistor temperature and rates of rise and fall of thermistor temperature were remarkably similar to those in which the thermistor was in the animal's cloaca. It was concluded that the temperature of a thermistor on the back of an animal was at a temperature close to that of the animal. The animal was scored as being inside its refuge if the thermistor temperature fell below 27 C and did not cycle with the air conditioner.

4.2.3.3 <u>Duration of experiments</u>. The diurnal exposure pattern of some individuals took several days to stabilise and animals were run in the apparatus for at least one week or until a stable exposure pattern was displayed.

4.2.3.4 Graphical presentation of results. Results are presented in the form of the percentage of the total time available that an animal was exposed at different times of the day. In the figures describing exposure, the abscissa is different times of the day, the ordinate the percentage of days on which the animal was exposed. In some cases, where figures combine results from more than one individual, all animals are represented by their exposure patterns measured over the same number of days, and these individual results are then summed for the whole.

The following terms are used in reference to various parts of the day.

(i) Day. The 24 hour period from midnight to midnight.

(ii) Dawn. The first period during the day when red heat lamps were switched on.

(iii) Daytime. The period after dawn when white heat lamps were switched on. The daytime can be divided into morning and afternoon.

(iv) Dusk. The period after the daytime when red heat lamps were on.

(v) Daylight hours. The period from the beginning of dawn to the end of dusk.

(vi) Evening. The period lasting a few hours after dusk.

(vii) Nightime. The part of the day other than the daylight hours.

4.2.3.5 Measurement of preferred body temperature. The preferred body temperature (PBT) was the mean of the body temperatures measured once every 15 minutes when the animal was exposed. If an animal was judged as not being exposed by the criteria described in S4.2.3.2, body temperature records from the time the animal first moved into its refuge until its body temperature had returned to about the preferred level were discarded. In some cases where an animal was exposed continuously its mean body temperature was lower in the morning than in the afternoon. Since some species consistently retreated to their refuges during the morning, their PBTs could be biassed upwards in relation to a species which was continuously exposed. To eliminate this possible bias, body temperatures for the calculation of preferred body temperatures were taken only from the period 1300 hours to the end of dusk (see also S4.2.3.6).

4.2.3.6 Statistical treatment of body temperature measurements.

Statistical treatment of consecutive body temperature measurements to determine whether different PBTs are selected is difficult unless it can be shown that the individual measurements are independent (i.e., uncorrelated). Correlation could exist either between successive 15 minute readings, or between PBTs on successive days. I tried to minimise correlation between successive readings by
(i) recording at 15 minute intervals. Examination of temperature records showed that 15 minutes was apparently long enough to make successive readings independent of short term fluctuations in body temperature.
(ii) Recording during the afternoon only. In some animals the mean body temperature was lower in the morning than in the afternoon, and correlation between measurements would result if data taken over the whole daytime period were used (see also S4.2.3.5). However, an animal's body temperature would sometimes remain fairly constant over a number of hours, and such periods did not appear to be predictable either in duration or the time of day they occurred. Correlation could be reduced by increasing the interval between successive readings (say to two hours), but would probably still exist. Also, increasing the interval between readings to about two hours would drastically reduce the number of degrees of freedom.

Examination of the PBTs measured on successive days showed that these were frequently correlated, and could remain so for up to about one week. Correlation between daily PBTs could only be eliminated by leaving an interval of say three to four weeks between daily replicates. Inordinately extensive facilities would be required to conduct experiments in this manner, since I considered it desirable to use animals kept in the surroundings in which they were tested (Heath, 1965, reported that abnormally high or low temperatures for a given thermoregulatory response occurred in animals during the first day in a new environment). Furthermore, the correlations themselves were thought to be of interest, necessitating continuous recording.

My method of collecting measurements at 15 minute intervals on successive days was therefore a compromise between the conditions required for rigorous statistical analysis and the demands imposed by limited facilities.

A nested analysis of variance is the appropriate statistical test to determine whether or not PBTs differ between species, between individuals within species or between days within individuals. Analysis of variance (anova) assumes independence of readings. The effect of correlation is to reduce the number of degrees of freedom, since readings are not independent. Thus the number of degrees of freedom in an analysis including correlated readings is overestimated, and this could result in an observed difference being spuriously judged significant. On the other hand, anova is the most sophisticated testing method for dealing with samples within samples (nested samples), and has the advantage of simultaneously considering all the data. The statistical approach I used was to perform an anova of the complete data, and then to check the conclusion reached at each stage of the anova by other methods to see if correlation was likely to have given spurious significance levels.

4.2.4 High temperature regime.

4.2.4.1 Experimental conditions. The environment used is illustrated in Figure 23. The outside area was sand; the thermal refuges were made from plaster of paris with dimensions as shown. Light and heat were supplied by white 250 watt heat lamps. Three different heat and light regimes were used and are summarised in Figure 24.

In the first, the air conditioner maintained an air temperature of 15 C at night. During the 12 hour long daytime, the air conditioner's cooling unit was switched off and outside air from within a corridor of the Zoology Department building was blown unmodified into the room. The Zoology Department is not air conditioned. When the cooling unit switched off, six heat lamps were switched on, one per pen. The radiant heat was fairly uniformly distributed over the pen, the only shady areas being the shadows cast by the refuges. The air temperature rose throughout the daytime, reaching 30 - 35 C before the lamps switched off and the cooling unit switched on. Ground temperatures rose to over 50 C except near the food containers which were sheltered by a ridge of sand; this ridge did not provide significant shelter for the lizards. The coldest parts of the refuges were at about 21 C (lower refuge) and 18 C (upper refuge) at heat on and about 25 C (lower) and 30 C (upper) at heat off. The lower refuge was thus well insulated against temperature fluctuations; however, near the entrance of the refuge the diurnal temperature fluctuations became more accentuated. Throughout the daytime and early evening animals were able to thermoregulate at their preferred body temperature by a variety of means. When the lights were first switched on, radiant energy was used to elevate body temperature to the preferred level. As air and ground temperatures increased and continuous exposure to radiation became impossible, the animal would either resort to shuttling between its refuge and the outside environment or to positioning itself in the small area of shade cast by the refuge. Eventually, outside conditions usually became so hot that the animal emerged infrequently or not at all, maintaining its body temperature at the preferred level within the refuge. After the lights switched off and the cooling unit switched on, the outside air temperature quickly fell below the refuge temperature and exposure resulted in a fall in body temperature. The body temperature could be maintained at the preferred level for one to two hours within the refuge before the refuge cooled. Occasionally, the air temperature remained above 15 C at night due to malfunction of the cooling unit. Water and food were made available at varying intervals.

The second heat and light regime was the same as the first except for the presence of a simulated dawn and dusk. Two white heat lamps switched on for 1½ hours constituted dawn, then an additional six white lamps came on for the daytime. The six lamps switched off 12 hours after they had switched on. The two lamps remained on for an additional 40 minutes and this constituted dusk. The air conditioner's cooling unit switched on after dusk and off at the beginning of dawn, blowing in outside air during the daytime. Environmental temperature levels were slightly higher than in the first regime. The distribution of heat by the two lamps switched on during dawn and dusk was uneven, but heat levels during the dawn period were insufficient for the preferred body temperature to be reached in any pen. The body temperature could be maintained at the preferred level at dusk owing to the higher air, ground and refuge temperatures existing at this time. Water was continuously available and food intermittently so.

The third heat and light regime was the same as the second except that the cooling unit of the air conditioner was not switched on for $1\frac{1}{2}$ hours after dusk or for $1\frac{1}{2}$ hours before dawn; during these periods, and the daytime, outside air was blown in. Temperature levels were similar to the second regime at times other than before dawn and after dusk. Air temperatures rose from 15 C to about 20 C before dawn, and remained at about 30 C after dusk before the cooling unit came on. Food and water were continuously available.

The first regime seemed to be significantly cooler than the other two. The heat levels in the second and third high temperature regimes were similar, except that just before dawn and just after dusk air temperatures in the third regime were higher than those in the second. Daily and seasonal variations in the temperature of the air blown into the room during the daytime and in the heat load conducted into the experimental room through the walls resulted in some day to day variation in temperature. It was not feasible to obtain more realistic or more reproducible sequences of temperature changes than these, or to obtain night time air temperatures below 15 C, the limit to the cooling of the air conditioner.

4.2.4.2 Determination of diurnal exposure pattern. In the high temperature regimes it was possible for animals to attain their preferred body temperatures inside their refuges during parts of the daytime, and photography was the only reliable method for measuring exposure patterns. In animals weighing less than about 15 g, insertion of the large twinflex leads into the cloaca produced changes in the diurnal exposure pattern, and photography and thermoregulation data from small animals bearing thermistors with large leads were discarded. Cloacal insertion of the smaller thermistor leads, used for some of the high temperature regime work and for all the thermal gradient regime work, produced no detectable changes in exposure patterns.

Diurnal exposure patterns are presented graphically as described in S4.2.3.4. The terms used to describe various parts of the day are the same as described in S4.2.3.4 with the following exceptions: dawn is the first period during the day during which two white heat lamps were switched on; daytime is the period during the day when six or eight white heat lamps were switched on, and dusk is the period after the daytime during which two white heat lamps were switched on.

The following terms are used in the next sections:

Refuge avoiding.	The animal tends to emerge from its refuge and be exposed.
Refuge seeking.	The animal tends to move into its refuge.
Thermophilia.	The animal tends to maintain its body temperature at the preferred level.
Thermophobia.	The animal tends to reduce its body temperature below the preferred level.

4.2.4.3 Comparison of diurnal exposure patterns in the high temperature regimes. As a result of the differences between the regimes and the seasonal differences in air temperature etc., the exposure patterns obtained for different individuals are not directly comparable. They can, however, be compared for the shape of the curve describing percentage exposure at different times of the day. When temperatures outside the refuges were too high to allow continuous exposure of the whole body, the refuges were warm enough, or almost warm enough, for the preferred body temperature to be reached inside the refuge without the animal emerging at all. Animals differed in their response to the presence of warm refuges and of abroad temperatures too high to permit continuous exposure; some emerged intermittently, while others did not emerge fully but positioned themselves in the zone of their refuges in which they were at their preferred body temperatures. The two basic responses to high environmental temperatures gave rise to three different curves describing exposure. Animals which emerged intermittently were sighted throughout the daytime with a frequency decreasing from the end of dawn to the beginning of dusk (see Figure 25). Animals which gradually moved back into their refuges were continuously exposed up to the point when they retreated beyond the range of the camera, but not at all after that, even though they might be only barely inside their refuge (see Figure 26). Some animals showed a combination of the two extremes, emerging intermittently during the morning but thermoregulating inside their refuges during the afternoon; this gave rise to an exposure pattern similar to Figure 27. The exposure curve drawn in Figure 25 was drawn on the basis of the following physical considerations. Exposure results in an increase in body temperature, the rate of increase increasing throughout the daytime; thus periods of exposure can only occur if the animal is able to cool itself inside its refuge. However, as refuge temperatures increase throughout the daytime also, animals will be able to cool themselves by a lesser amount, and will take longer doing it, as the daytime progresses. The faster rates of heating outside the refuge and the slower rates of cooling inside the refuge will result in smaller proportion of the time being spent exposed. However, the animal would be able to spend a proportion of the time exposed throughout the daytime, since the coolest parts of the refuges stayed well below the preferred body temperature throughout the day.

4.2.5 Body weights of lizards.

The experiments using the high temperature regimes were carried out before those using the thermal gradient regime. During the gradient studies and some of the experiments using the third high

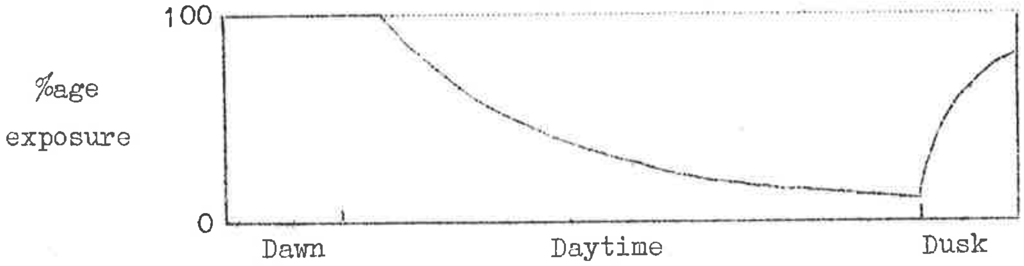


Figure 25. Predicted mean diurnal exposure pattern of an animal emerging intermittently in the high temperature regime. Exposure is represented by the area under the curve. Predawn and postdusk exposure is not considered.

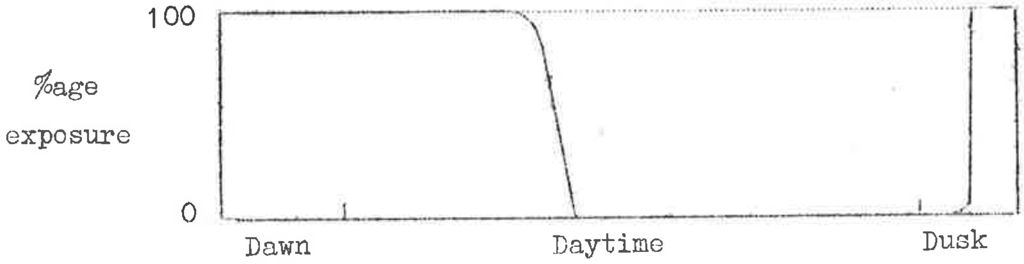


Figure 26. Predicted mean diurnal exposure pattern of an animal retreating gradually as environmental temperatures rise in the high temperature regime. Exposure during dusk will depend on environmental temperatures falling sufficiently to permit emergence. Exposure is represented by the area under the curve. Predawn and postdusk exposure is not considered.

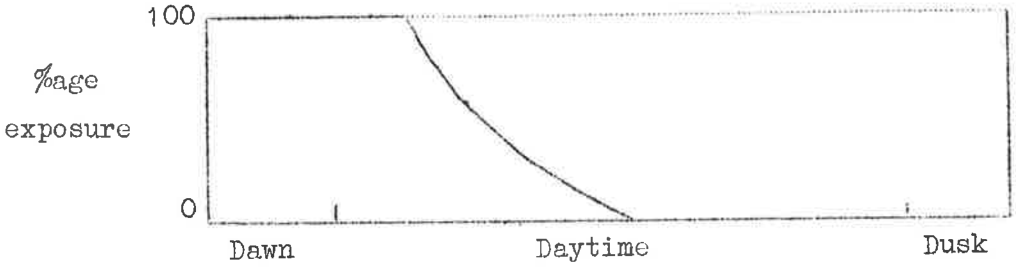


Figure 27. Predicted mean diurnal exposure pattern of an animal in the high temperature regime which emerges intermittently during the morning but retreats to its refuge during the afternoon and dusk if the refuge is warm enough for body temperatures at the preferred level to be reached within it. Exposure is represented by the area under the curve. Predawn and postdusk exposure is not considered.

temperature regime it was possible to calculate the weight of the animals by weighing the animals together with their thermistor leads. The number of mealworms eaten was counted every day. Samples of 50 mealworms were weighed on a number of occasions, and the average weight of a mealworm was consistently found to be about 0.12 g. It was possible to infer the amount of water consumed in cases where the animal increased in weight by more than would be expected on the basis of its food consumption and the estimated water loss per day (this varied between animals and was usually in the range 0.1 - 0.25 g/day; it was estimated from the most common weight loss occurring in the absence of food consumption and, it is assumed, drinking. It is a very rough estimate and cannot be realistically compared with the rates of evaporative water loss measured under standard conditions). This method will obviously underestimate water consumption as no allowance can be made for water consumed on a day when the animal excreted an equal or greater weight of urine and/or faeces. Although it was not possible to determine every day on which water was drunk, it was possible to determine at least some.

4.3 RESULTS

4.3.1 Preferred body temperatures.

4.3.1.1 Variations between and within species in PBT. Preferred body temperature data were collected for Egernia whitei, E. margaretae, E. multiscutata, E. inornata, E. striata and E. kintorei. The PBT of an animal is the mean of all the individual body temperature records. The PBTs of the individuals tested are shown in Table 15. Anova showed that there were no significant differences in PBT between the species but that there were highly significant differences from animal to animal and from day to day. The anova is summarised in Table 16. The conclusion that there were no significant differences between species was tested by an anova using the PBTs shown in Table 15; correlation within the sample for each individual has no effect on this anova, since only one value per animal is used. The conclusion was the same and this anova is summarised in Table 17.

Table 15. Preferred body temperatures of the *E. whitei* species-group. Each temperature shown was obtained from one animal. The number in parentheses is the number of days the run was continued. The number of records per day was usually 20 - 30. Abbreviations of the species and population names are: *m. marg* = *E. m. margaretae*, *m. pers* = *E. m. personata*, *multi* = *E. multiscutata*, *inorn* = *E. inornata*, *kint* = *E. kintorei*. Blk Mt = Black Mountain, Rem Rk = Remarkable Rocks, Wedge = Wedge Island, Pt Ger = Port Germein Gorge, Telow = Telowie Gorge, Mid G = Middle Gorge, Wilp = Wilpena, Ital G = Italowie Gorge, St Fr = St Francis Island, Pt Lin = Port Lincoln.

whitei	*m. marg*	*multi*	*inorn*	*striata*	*kint*
Rem Rk	33.53 (35)	Rem Rk	33.34 (3)	32.91 (31)	33.37 (21)
33.90 (14)	*m. pers*	33.81 (13)	33.79 (3)	33.28 (17)	33.83 (28)
Blk Mt	Pt Ger	34.47 (9)	34.12 (10)	34.07 (25)	
32.93 (18)	31.98 (13)	Pt Lin	34.55 (7)	34.38 (11)	Species mean = 33.60 (49)
32.99 (4)	32.22 (6)	35.03 (8)	34.58 (9)	Species mean = 33.66 (84)	
33.78 (29)	32.93 (23)	St Fr	35.07 (6)		
34.24 (20)	33.11 (24)	32.88 (4)	Species mean = 34.24 (38)		
Wedge	34.18 (6)	34.17 (20)			
33.81 (31)	Telow				
34.92 (6)	34.47 (32)	Species mean = 34.14 (54)			
Species mean = 33.80 (122)	Mid G				
	32.55 (33)				
	33.10 (7)				
	Wilp				
	33.04 (21)				
	Ital G				
	33.03 (5)				
	33.78 (10)				
	m. pers mean = 33.13 (180)				

Table 16. Analysis of variance of the preferred body temperatures of the *Egernia whitei* species-group. Data from *E. whitei*, *E. margaretae*, *E. multiscutata*, *E. inornata*, *E. striata* and *E. kintorei* are included. *E. m. margaretae* and *E. m. personata* are treated as separate species.

Source of variation	d.f.	Sum of squares	Mean square
Species	6	1560.45	260.07
Animals in species	29	5917.18	204.04
Days in animals	526	7595.44	14.44
Determinations in days	15906	27048.89	1.70

Test for differences among species: $F(6,29) = \frac{260.07}{204.04} = 1.27$ Not sig, $(p > 0.25)$

Test for differences among animals: $F(29, 526) = \frac{204.04}{14.44} = 14.1$ Sig, $(p < 0.001)$

Test for differences among days: $F(526,15906) = \frac{14.44}{1.70} = 8.49$ Sig, $(p < 0.001)$

Table 17. Analysis of variance of the differences in PBT between species in the *Egernia whitei* species-group. Each animal is represented by a single value, taken from Table 15.

Source of variation	d.f.	Sum of squares	Mean square
Species	6	6.190	1.03
Animals in species	29	14.777	0.51

Test for differences between species:

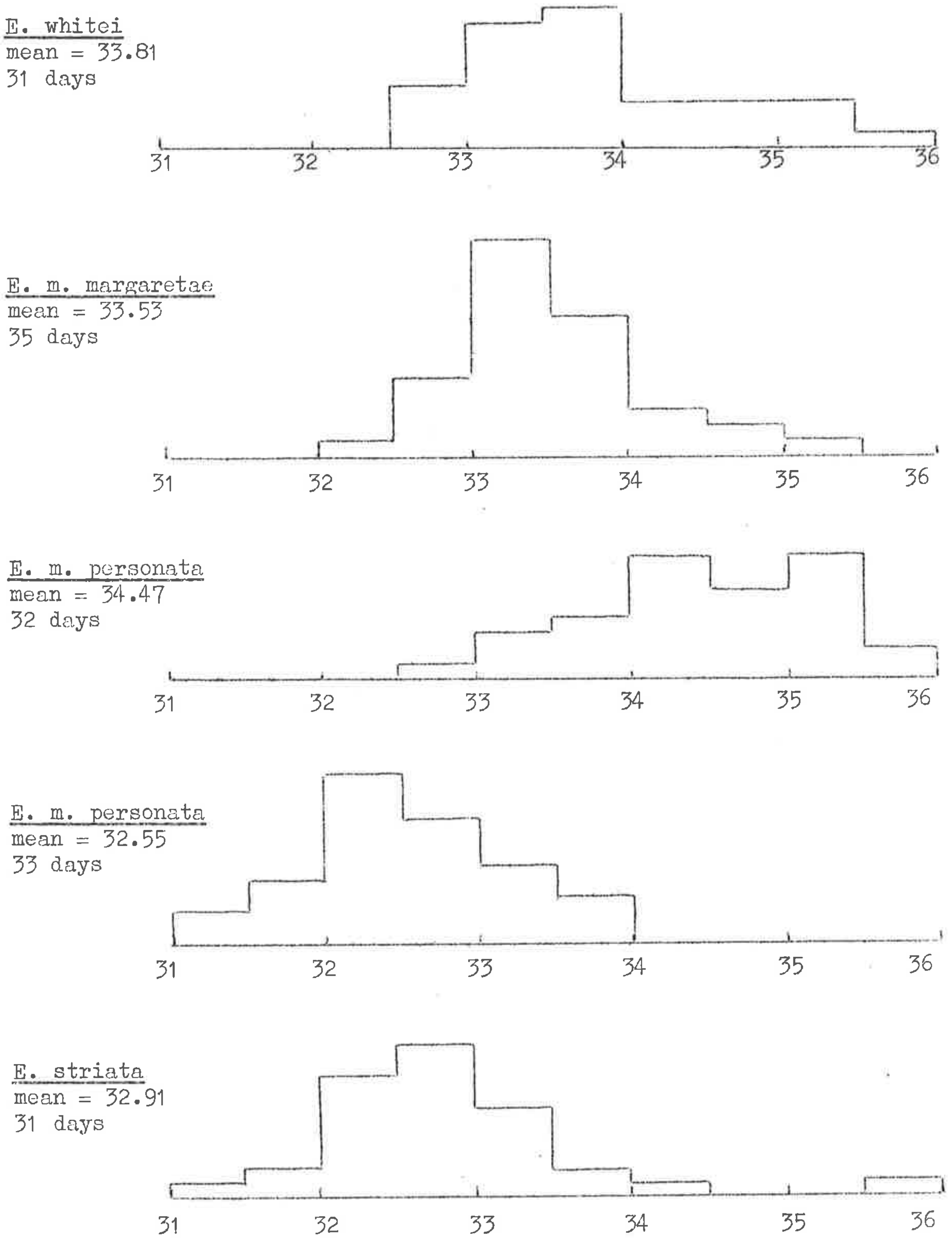
$F\ (6,29) = \frac{1.03}{0.51} = 2.02$ Not significant, p = *ca* 0.1

Although the differences among species in PBT are not statistically significant, there was a tendency for the PBT to decrease as the maximum size attained by the species increases, and this trend was present in both the rock living and sand burrowing species. The PBTs of the different species are shown in Table 18 arranged according to refuge preference and maximum attained size.

Table 18. Preferred body temperatures of the Egernia whitei species-group in relation to refuge preference and maximum attained size. The data are taken from Tables 2 and 15. The differences between the species in PBT are not statistically significant.

Species	E. whitei	E. m. margaretae	E. m. personata	E. inornata	E. multiscutata	E. striata	E. kintorei
Refuge preference	Rock	Rock	Rock	Sand	Sand	Sand	Sand
Maximum SVL (mm)	101	107	107	84	94	117	206
PBT (C)	33.80	33.53	33.13	34.24	34.14	33.66	33.60

The values of the F ratios appearing at the bottom of Table 16 in the tests for differences among animals and differences among days are so great that about 99% of the degrees of freedom would have to be lost by correlation before the results became non-significant, and this is unlikely. Nevertheless, the conclusion drawn from Table 16 that animals within species differ in their PBT was checked. Since the PBTs on successive days were correlated, and the PBT would remain at a high, or a low, level for about a week, measurement periods of several weeks would be required to ensure that the range of daily PBTs measured in a single animal represented the full range of PBTs likely to be displayed by that animal. Five animals were run in excess of 30 days, and histograms showing the distributions of their daily PBTs are shown in Figure 28. It appears most unlikely that these samples would have been drawn from one population,



E. whitei
mean = 33.81
31 days

E. m. margaretae
mean = 33.53
35 days

E. m. personata
mean = 34.47
32 days

E. m. personata
mean = 32.55
33 days

E. striata
mean = 32.91
31 days

Figure 28. Distributions of daily preferred body temperatures of five animals run for more than 30 days each. Temperature in degrees centigrade. Number of days of records and mean of the individual body temperature measurements shown.

and the conclusion that animals have different PBTs appears valid. Regarding differences between days within animals in selection of PBT, about 70% of the consecutive body temperature measurements collected on any one day were distributed within 1.5 C of the mean for that day. It would seem very unlikely that differences between daily means consistently reaching 4 C would result from correlation between 15 minute readings on any one day, and the conclusion that an animal may have different PBTs on different days appears valid.

It is possible that the differences between individuals in selection of PBT are the result either of the animals being run at different times of the year, or of the length of time the animals had been in captivity. To test the former of these possibilities, the mean PBTs of the 36 animals tested were arranged according to the month in which they were obtained. A test of homogeneity of variance, and an anova, performed on the data thus arranged showed that there were no significant differences between months either in the variance between PBTs, or in the PBTs themselves, and it is concluded that the differences observed between the animals are intrinsic differences in the levels of their PBTs. The statistical tests are summarised in Table 19.

Table 19. Summary of tests for monthly differences in PBT selection among the *E. whitei* species-group.

(1) Test for homogeneity of variance within months. Bartlett's Test was used, as described in Snedecor (1961).

Chi-square with 6 d.f. = 2.58. Not significant, $0.9 > p > 0.75$

(2) Test for differences between months in level of PBT.

Source of variation	d.f.	Sum of squares	Mean square
Months	8	6.33	0.79
Animals in months	27	14.49	0.54

Test for differences between months:

$$F\ (8,27) = \frac{0.79}{0.54} = 1.46.$$ Not significant, $0.25 > p > 0.10$

To test the latter possibility, a Rank Correlation Test was performed on the respective PBTs and periods of captivity of 35 animals (the E. multiscutata from Port Lincoln was excluded since its collection date was uncertain). The test was performed as described in Siegel (1956), and gave a Kendall Rank Correlation Coefficient of 0.07, which is not significant statistically ($z = 0.59$, $p = 0.56$).

4.3.1.2 Influence of exposure, food and water on the preferred body temperature. No detectable correlations with PBT were observed in day to day variations in exposure, food consumption, body weight and calculated water consumption in healthy animals supplied with food and water.

If water was removed from an animal, its PBT was observed to fall (see Table 20). Comparing the PBTs of dehydrated animals with those of animals supplied with water (see Figure 29) it is evident that the PBT falls to levels well below those occurring in fully hydrated animals. The PBT was restored to normal levels upon rehydration (see Table 20 and Figure 29). Regarding the slight negative skewness shown in Figure 29, De Witt (1967) found that the distribution of individual temperature records about the mean for the day was also negatively skewed.

A comparable fall in mean body temperature was observed in animals dehydrated in the high temperature regimes. The fall in PBT in dehydrated animals would result either from the altered hormonal levels resulting from dehydration, or from the disturbed water and salt levels inside the body. Although one could not infer this from the data on food and water intake, body weight and PBT, the day to day variation in PBT in fully-hydrated animals might have its origin in some form of variation of the hormonal state of the animal, and the differences in PBT between individuals might be related to innate differences in the endocrinological constitutions of the animals.

Table 20. Changes in the PBT of *Egernia* upon dehydration in the thermal gradient regime. Results from five animals are shown (columns). Each figure represents the PBT of an animal for one day. The double black line across the page denotes the removal of water, and the single black line in each column rehydration. "nt" indicates that the animal did not thermoregulate on that day, "dead" indicates that the animal died. One animal moulted during the experiment.

E. m. personata	*E. m. personata*	*E. multiscutata*	*E. striata*	*E. kintorei*
34.49	32.47		32.99	32.87
33.59	32.73		32.46	33.46
33.99	32.77		33.04	34.01
33.75	32.39		32.38	32.40
35.20	32.81		33.08	32.42
35.13	33.87	34.53	32.92	32.37
34.95	moulted	34.32	32.59	32.81
34.52	31.34	33.34	32.23	32.45
33.70	30.50	33.81	32.18	31.67
33.32	30.00	32.45	31.72	nt
32.73	29.64	32.08	32.07	32.48
32.60	29.31	30.75	31.27	32.53
32.50	29.10	28.88	32.21	32.00
32.54	28.08	nt	31.19	30.39
31.29	30.27	dead	30.74	30.75
34.48	ca 26.0		30.76	nt
35.95	dead		30.31	nt
35.21			32.76	nt
34.83				
34.41				
35.34				

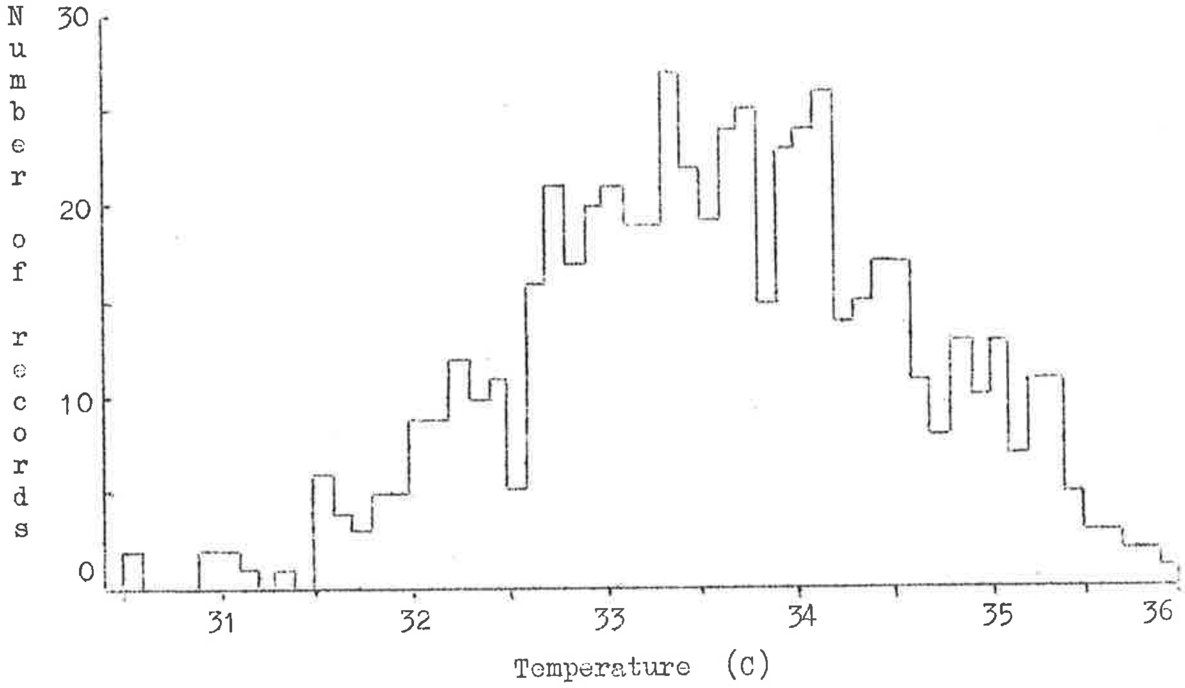


Figure 29. Frequency distribution of preferred body temperatures of the _Egernia whitei_ species-group. Data from _E. whitei_, _E. margaretae_, _E. multiscutata_, _E. inornata_, _E. striata_ and _E. kintorei_ were included. Data for 596 days were obtained from fed, fully hydrated animals in the thermal gradient regime. The shape of the curve might be influenced by correlation between the PBTs measured on successive days in any one animal, and as a result of different animals selecting different PBTs.

4.3.2 Role of temperature in emergence and retreat.

4.3.2.1 Emergence at dawn. In both the high temperature and thermal gradient regimes animals typically emerged about the time the heat lamps were switched on. It is interesting to note that some animals emerged slightly before the lamps were switched on (e.g., Figure 32a), suggesting that a diurnal rhythm is involved in emergence behaviour. Under similar experimental conditions, Heath (1962) observed emergence shortly before dawn in diurnal lizards of the genus *Phrynosoma*, and Pough (1969) observed a temperature independent increase in heart and breathing rates beginning one to two hours before dawn in the diurnal lizards *Uma notata inornata* and *Dipsosaurus dorsalis*. Cloudsley-Thompson (1965) showed that there were diurnal rhythms of activity (as distinct from exposure) in two species of tropical lizards. He found that animals were active at the same times of the day for several days after the animals had been placed in environments where the temperature, light and humidity were constant for the whole 24 hours. Cloudsley-Thompson (1965) has summarised the restricted literature on diurnal activity patterns of lizards. In the high temperature regimes animals emerged with body temperatures usually about 20 C, and with air temperatures of 15 - 20 C in the first and second high temperature regimes or 19 - 25 C in the third high temperature regime, these being the temperature levels at dawn in the respective environments. Since the temperature inside the animal's refuges did not start to increase for one to two hours after the heat lamps had been switched on, it is probable that increased light levels, rather than increased air temperatures in the outside environment, prompt emergence or set the internal clock. This is also suggested by the fact that in the third high temperature regime animals rarely emerged in the period after the air conditioner's cooling unit had been switched off and before the heat lamps had been switched on, although outside air temperatures rose by 4 - 8 C, whereas in the second and third high temperature regimes animals frequently emerged in the period after the two heat lamps had switched on, although body temperatures rarely rose above 25 C in this period. It is possible that emergence is dependent upon actual or impending conditions outside the refuge suitable for the animal to reach body temperatures at or close to the preferred level, and that increased light levels act as a clue to the advent of these conditions or are used to set the internal clock. The animal would probably have no clue to increasing outside environmental temperatures when the cooling unit was switched off in the morning in the third high temperature regime, as temperatures in the refuges were still falling in this period. In the thermal gradient regime animals usually emerged at or about the time heat lamps were switched on. Some animals (e.g., see Figure 33d) avoided exposure during the simulated dawn, even though they could have reached their preferred body temperature during this period.

4.3.2.2 Retreat at dusk. In most animals in the thermal gradient regime retreat at dusk occurred shortly after the heat lamps were switched off, but some animals (e.g., see Figures 33a, 34f) tended to avoid exposure for at least part of the dusk period. In contrast to the other species, E. kintorei remained exposed for several hours after dusk. In species other than E. kintorei, retreat usually occurred before the body temperature had fallen more than a couple of degrees below the preferred level. Since the lizards could maintain their body temperature at or close to the preferred level for about an hour after dusk by lying on the warm sand under the heat lamps, it appears that the decrease in light level prompts retreat. The decrease in light level at the beginning of dusk probably prompted the animals shown in Figures 33a, 34f to retreat during dusk.

In the high temperature regime animals sometimes emerged during dusk after having retreated during the daytime as environmental temperatures rose (see Figures 38a, 41, 43a). They usually then retreated when the lights went out at the end of dusk, although E. kintorei and a few individuals of other species remained exposed for a period after dusk. In the first and second high temperature regimes environmental temperatures and light levels outside the refuge fell rapidly after dusk, and it is not possible to attribute retreat to one or the other of these two variables. However, in the third high temperature regime, air and body temperatures fell slowly after dusk but the animals shown in Figures 42c, d, 43c, d, e still retreated soon after the lights went out, suggesting that in this environment, as in the thermal gradient regime, retreat occurs when light levels fall.

4.3.2.3 Midmorning retreat and emergence. In the thermal gradient regime, E. striata, E. kintorei, E. m. margaretae, E. whitei from American River and some specimens of E. inornata emerged at or about dawn, retreated at some point during the morning and then reemerged during the late morning or the afternoon; in E. m. margaretae and E. kintorei animals remained exposed throughout the day on some days. These results are illustrated in Figures 30c, 31, 34 - 36. It was thought that this retreat could be due to any of the following:
(i) refuge seeking becoming dominant to thermophilia, inducing retreat to the refuge even though body temperatures fell below the level otherwise preferred,
(ii) thermophobia becoming dominant to refuge avoiding,
(iii) the animal becoming both refuge seeking and thermophobic.
It was considered that either (i) or (iii) was more likely than (ii) since animals could remain exposed and yet reduce their body temperature to the same level as that found in the refuge (about 24 C) by moving to a cool part of the thermal gradient. To discriminate between these possibilities, two E. striata and one E. kintorei were provided with thermal gradients inside and outside their refuges during the daytime. It was found that the animals still retreated to the refuge after dawn (and now stayed there for most of the afternoon as well - see Figures 35f, g, 36f) and maintained their body temperature at a level slightly below that preferred in a photothermal gradient during the afternoon (see Table 21). It is concluded that the morning retreat shown by E. striata and E. kintorei in the thermal gradient and high temperature regimes results from refuge seeking becoming dominant to thermophilia, causing the animal to retreat to its refuge even though this might result in the body

Table 21. Mean body temperatures of two E. striata and one E. kintorei during the morning (0600 - 0900 hours) and afternoon (1300 - 2000) in the thermal gradient regime. Mean body temperatures are given for periods when there were thermal gradients both inside and outside the refuges, and when there were thermal gradients outside the refuges only. When there were no thermal gradients inside the refuges, the refuges were at about 24 C. The mean body temperatures of the E. striata during the morning were equal to the refuge temperatures (about 24 C), but the mean body temperature of E. kintorei during the morning (29.69 C) exceeded 24 C since the animal spent some of the morning outside the refuge at body temperatures greater than 24 C. Number in parentheses is the number of days measurements were taken.

		E. striata	E. striata	E. kintorei
Thermal gradient outside refuge	0600 - 0900	24.15 (7)	24.50 (8)	29.69 (8)
	1300 - 2000	33.90 (7)	33.56 (8)	33.17 (8)
Thermal gradient inside and outside refuge	0600 - 0900	32.21 (5)	32.55 (8)	32.38 (8)
	1300 - 2000	33.65 (5)	33.43 (8)	34.09 (8)

temperature falling. The lowest body temperature to which animals were subjected by this refuge seeking was 24 C; whether they would still retreat if compelled to tolerate lower body temperatures inside their refuges was not determined. In the thermal gradient regime the lizards emerged again at about midday after the morning retreat, apparently when the dominance of thermophilia by refuge seeking was reversed. If the animals were given a thermal gradient inside their refuges during the daytime, E. striata was refuge seeking all day except occasionally before dusk, when the animal emerged, while E. kintorei showed refuge seeking for a prolonged period during the middle of the daytime, but was exposed during the late afternoon (see Figures 35f, g, 36f). In all the experiments using thermal gradients emergence at dawn or dusk occured in a low light intensity.

It is unfortunate that a shortage of time prevented ~~me~~ my conducting more experiments using thermal gradients inside the refuges in the thermal gradient regime. Such experiments, taken in conjunction with those performed in the thermal gradient regime with no refuge gradients, would have allowed a comparative and more detailed study of the relations between refuge seeking and thermophilia. Although some of this information can be gleaned from the experiments in the high temperature regime, it is incomplete because the animals could regulate their body temperatures at the preferred level inside the refuge only during the afternoon and late morning. Also, during the afternoon in the high temperature regime, the environment outside the refuge was not a thermal gradient but was one in which the heat levels were so high that animals could spend only a portion of the time exposed, resulting in some confusion in determining whether the response shown was refuge seeking or thermoregulatory.

Insufficient data exist to determine whether or not intermittent retreat was a refuge avoiding response, and I have assumed this to be true. Later during the day, if the animal retreated very deep into its refuge and remained there, it would appear that the response was refuge seeking in relation to an animal which emerged intermittently and which was therefore still occasionally exposed. The data obtained with *E. striata* and *E. kintorei* in the high temperature regime and the thermal gradient regime with thermal gradients inside the refuges support this latter suggestion. Thus *E. striata* remained inside its refuge during the late afternoon in the high temperature regime and was refuge seeking during the same period in the thermal gradient regime if the refuge had a thermal gradient inside. *E. kintorei* emerged intermittently during the late afternoon in the high temperature regime, and was exposed (refuge avoiding) in the thermal gradient regime if there was a thermal gradient inside the refuge.

4.3.2.4 *Daytime retreat in the high temperature regime*. Lizards retreated to their burrows at any time of the daylight hours when abroad environmental temperature levels became very high, and also sometimes if they could maintain body temperatures at about the preferred level inside their refuges. From the previous pages it is apparent that frequently retreat to the refuge was not occasioned by high temperatures outside the refuge or by warm refuges but by refuge seeking becoming dominant to thermophilia. Thus the body temperatures of *E. striata* and *E. kintorei* fell to about 25 C, and those of *E. m. margaretae* to about 27 C, immediately following retreat to the refuge during the early morning. The body temperatures rose to the preferred level as the refuges warmed. In other species it is possible that as outside temperatures rise the animal retreats to its refuge (either intermittently or gradually) so as to maintain its body temperature at the level preferred in a thermal gradient, i.e., the requirements of thermophilia and refuge avoiding are met simultaneously. Alternatively, it is possible that refuge avoiding becomes dominant to thermophilia at this point and the animal tolerates body temperatures above its preferred level so as to remain exposed for a greater proportion of the time (the term "thermophilia" becomes inappropriate at this point, but is retained owing to the lack of a suitable alternative). Other workers (e.g., Cowles and Bogert, 1944; Heath, 1965; Bradshaw and Main, 1968) have observed that as environmental temperatures rise some lizards tolerate elevated body temperatures, apparently to prolong exposure, and Bradshaw and Main have shown that these elevated body temperatures are above the level preferred in a thermal gradient. The tolerance of elevated body temperatures is usually correlated with the adoption of specific body postures which reduce the radiant and conducted heat load. Many species in the *Egernia whitei* species-group are refuge seeking, and data ~~is~~ are available for only two animals which can test this point (an *E. m. personata* and an *E. slateri*). Mean body temperatures were measured during two periods for each animal: after emergence, and before retreat (in *E. slateri*) or during intermittent emergence (in *E. m. personata*). The results, presented in Table 22, show that there were no large differences between the mean body temperatures at these times, and it is concluded that in these two animals refuge avoiding was not dominant to thermophilia.

Table 22. Mean body temperatures of an *E. slateri* and an *E. m. personata* in the high temperature regime. Measurements taken on five days at 15 minute intervals for two hours after emergence in the morning and before retreat to the refuge (in *E. slateri*) or during intermittent emergence in the afternoon (*E. m. personata*).

		day 1	day 2	day 3	day 4	day 5
E. slateri	MBT after emergence.	33.7	34.1	32.5	32.3	34.2
	MBT before retreat.	32.8	33.5	32.9	34.9	34.2
Mean MBT after emergence =		33.4				
Mean MBT before retreat =		33.7				
E. m. personata	MBT after emergence.	32.6	32.6	33.5	33.4	33.0
	MBT during intermittent emergence.	30.5	32.0	32.9	32.7	33.6
Mean MBT after emergence =		33.0				
Mean MBT during intermittent emergence =		32.3				

4.3.3 Diurnal exposure pattern: thermal gradient regime.

The diurnal exposure patterns did not appear to be influenced either by length of captivity or by the time of year the results were obtained.

4.3.3.1 Terminology. The proportions of time spent outside the refuge at different times of the daylight hours by individuals of different populations and species were used to compare diurnal exposure patterns. These patterns can be divided into three types; the words underlined will be used in future reference to these types.

(i) *Continuous exposure* from about dawn until about dusk, or until after dusk. See Figure 30a.

(ii) *Delayed emergence*, or *early retreat*. The animal remains in its refuge for varying periods during and after dawn, or retires to its refuge before and during dusk. Exposure during the rest of the daylight hours is usually continuous. See Figures 35a, 32e.

(iii) *Discontinuous exposure*, where the animal emerges briefly at dawn and then retires to its refuge for a variable period before emerging for the rest of the daylight hours and possibly part of the evening. See Figure 30c.

4.3.3.2 *Diurnal exposure pattern of Egernia whitei*. Eleven animals were tested, from Wedge Island (2 animals), Black Mountain (4) and American River (5). The animals from Wedge Island and Black Mountain were continuously exposed with very little variability within either population, the results being shown in Figure 30a - b. Wedge Island animals remained exposed slightly longer after dusk than Black Mountain animals. The American River sample showed a discontinuous exposure pattern (see Figure 30c); all animals were similar.

4.3.3.3 *Diurnal exposure pattern of Egernia margaretae*.

E. m. margaretae. One animal from Reedy Creek Rockhole was tested. It had a slightly discontinuous exposure pattern, the result being shown in Figure 31. The animal frequently remained exposed throughout the daylight hours.

E. m. personata. The diurnal exposure patterns of 14 individuals from five populations were determined. These were

Italowie Gorge	3 animals
Wilpena	1 animal
Middle Gorge	4 animals
Port Germein Gorge	5 animals
Telowie Gorge	1 animal.

The exposure patterns were continuous, or nearly so.

Italowie Gorge. The three animals tested showed continuous exposure patterns, all being very similar. See Figure 32a.

Wilpena. The one animal tested was continuously exposed, the result being shown in Figure 32b.

Middle Gorge. Of the four animals tested, two showed continuous exposure while the other two occasionally retired to their refuges for periods of about 30 minutes throughout the daylight hours. The exposure pattern of the individual with the greatest interruption of exposure is shown in Figure 32c, and that of the sample as a whole in Figure 32d.

Port Germein Gorge. Five animals were tested, two being continuously exposed while the other three showed a slight restriction of exposure. Figure 32e shows the result for the animal with the most extensive restriction of exposure, and Figure 32f the result for the whole sample.

Telowie Gorge. The continuous exposure pattern of the single animal tested is shown in Figure 32g. Dehydration resulted in a decrease in exposure: see Figure 32h.

4.3.3.4 Diurnal exposure pattern of *Egernia multiscutata*. Eight specimens were tested, three from St Francis Island, three from Marion Bay and two from Remarkable Rocks. The diurnal exposure patterns of some individuals took up to three weeks to stabilise. All animals were run until stable patterns were obtained.

St Francis Island. The three animals showed continuous exposure patterns. One of the animals tended to retreat to the refuge during dusk; the results from this animal and the sample as a whole are shown in Figure 33a - b.

Marion Bay. Two of the three animals were continuously exposed. The third alternated between spending a number of days continuously exposed followed by a number of days of early retreat. Results are shown for both phases of this animal's behaviour, for the other two animals combined, and for the whole sample (see Figure 33c - f).

Remarkable Rocks. One of the two animals showed early retreat on some days, the other a slightly discontinuous exposure pattern. The results are shown separately in Figure 33g - h.

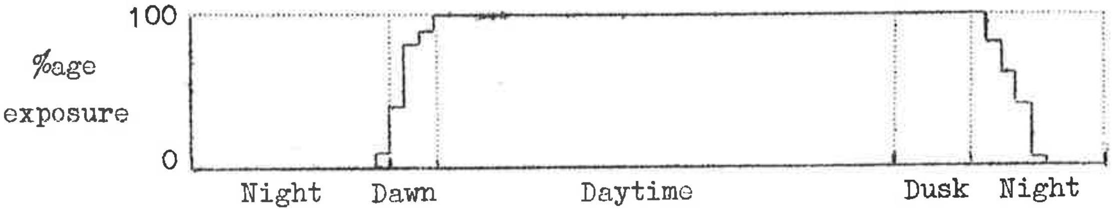
4.3.3.5 Diurnal exposure pattern of *Egernia inornata*. Six animals from Renmark were tested. There was considerable variability among individuals, and the results are shown both for the individuals and for the whole sample in Figure 34. There was restriction of exposure at dawn, during the early morning, and in one animal at dusk.

4.3.3.6 Diurnal exposure pattern of *Egernia slateri*. When the thermal gradient studies were being conducted, no specimen of *E. slateri* was available for testing. From data presented in S4.3.4.5 and obtained in the high temperature regime it appears that in the thermal gradient regime *E. slateri* would show continuous exposure.

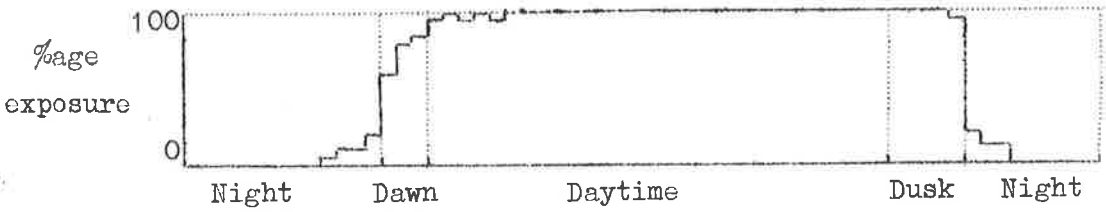
4.3.3.7 Diurnal exposure pattern of *Egernia striata*. Four animals from Chilla Well were tested. Three showed a discontinuous, and one a delayed emergence, exposure pattern. The individual results, and the mean for the sample, are shown in Figure 35a - e. Two animals were provided with a thermal gradient inside their refuges as well as photothermal gradients outside, and the exposure patterns obtained are shown in Figure 35f - g. There was a substantial reduction in exposure during the daytime, the animals maintaining body temperatures close to the preferred level within their refuges (see S4.3.2.3).

4.3.3.8 Diurnal exposure pattern of *Egernia kintorei*. Four animals from Aileron were tested, and all showed discontinuous exposure. As there was some variability the individual results are shown as well as the mean in Figure 36a - e. One *E. kintorei* was provided with a refuge thermal gradient in addition to a photothermal gradient outside its refuge, and the resulting exposure pattern is shown in Figure 36f. It can be seen that the period of retreat was prolonged from the morning to include the early afternoon as well. The animal maintained body temperatures at about its preferred level during the period of retreat (see S4.3.2.3).

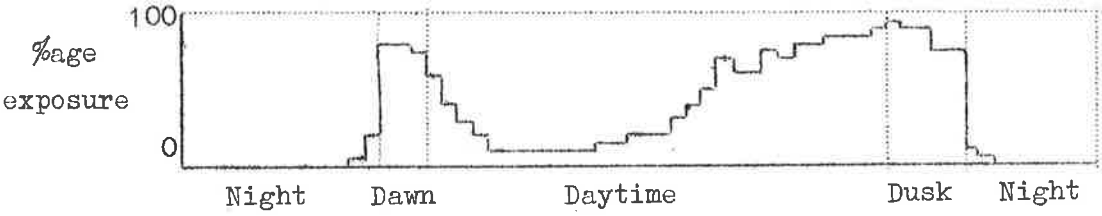
4.3.3.9. Influence of food and water intake on diurnal exposure pattern. No correlation between the amount of food consumed and the



(a) Wedge Island. n = 2.



(b) Black Mountain. n = 4.



(c) American River. n = 5.

Figure 30. Diurnal exposure pattern of E. whitei in the thermal gradient regime. The two animals from Wedge Island were tested for 9 and 25 days respectively, the four from Black Mountain for 8, 15, 15, 19 days respectively and the five from American River for 15, 40, 50, 50, 50 days respectively. Data collected after exposure pattern had stabilised - see S4.2.3.3.

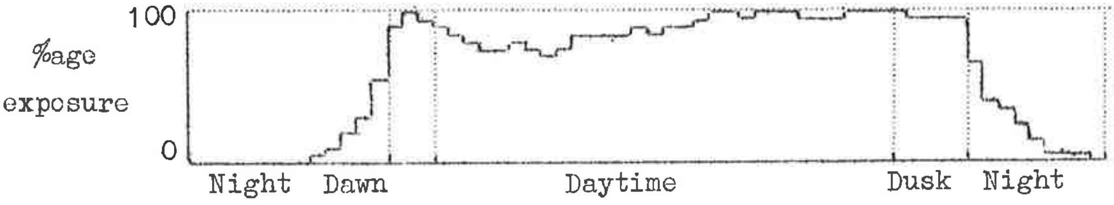
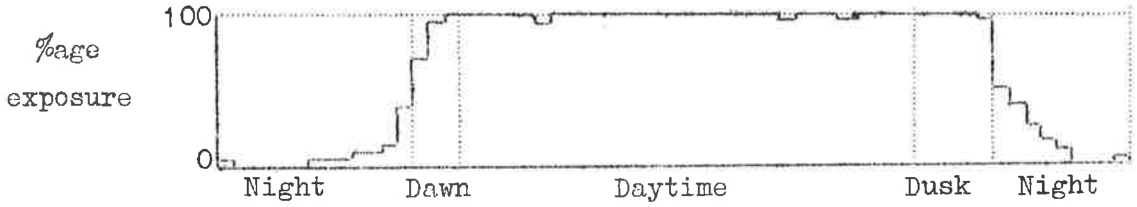
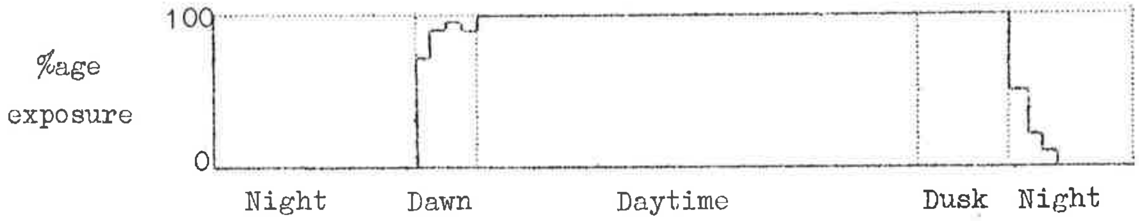


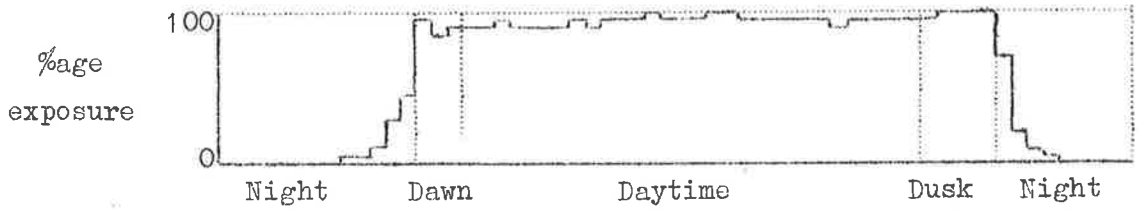
Figure 31. Diurnal exposure pattern of E. m. margaretae from Reedy Creek Rockhole. One animal was tested for 30 days. Data collected after exposure pattern had stabilised - see S4.2.3.3.



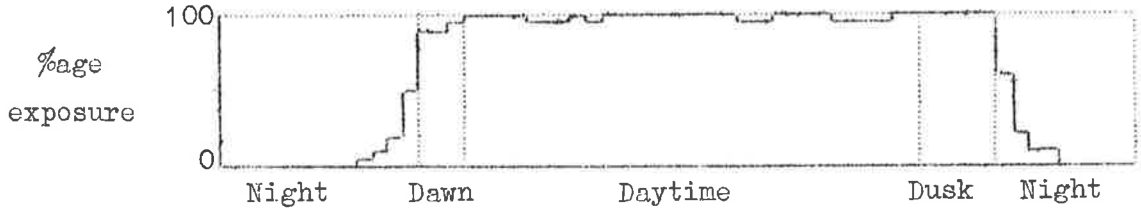
(a) Italowie Gorge. n = 3



(b) Wilpena. n = 1.

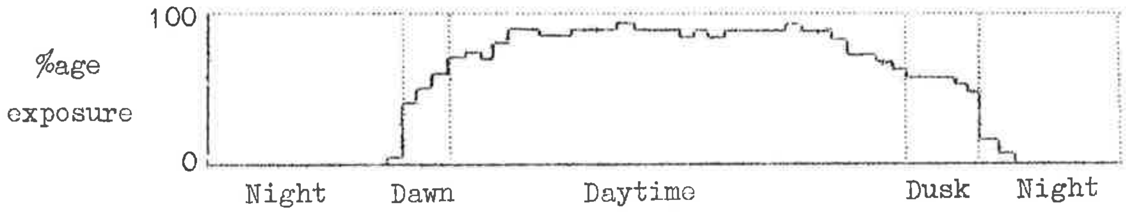


(c) Animal from Middle Gorge with greatest restriction of exposure.

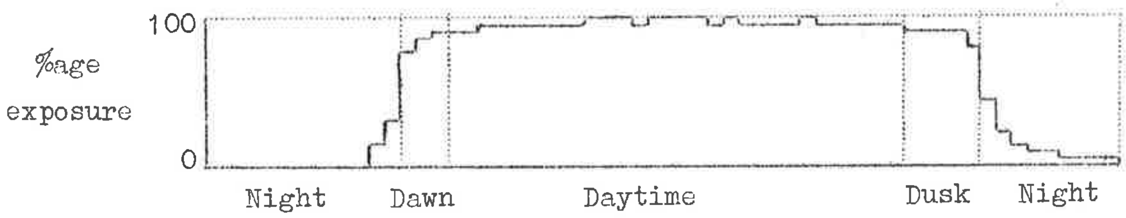


(d) Middle Gorge. n = 4

Figure 32. Diurnal exposure pattern of _E. m. personata_ in the thermal gradient regime. See also next page. The three animals from Italowie Gorge were tested for 10 days each, the animal from Wilpena for 20 days, the animal from Middle Gorge shown in (c) for 25 days, and the four animals from Middle Gorge for 10, 20, 25, 25 days respectively. Data collected after exposure pattern had stabilised - see S4.2.3.3.

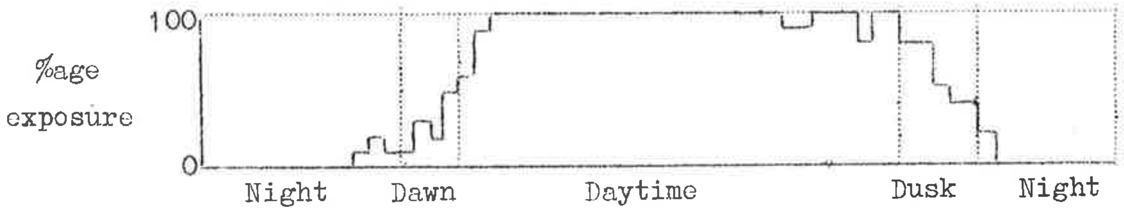


(e) Animal from Port Germein Gorge with greatest restriction of exposure.



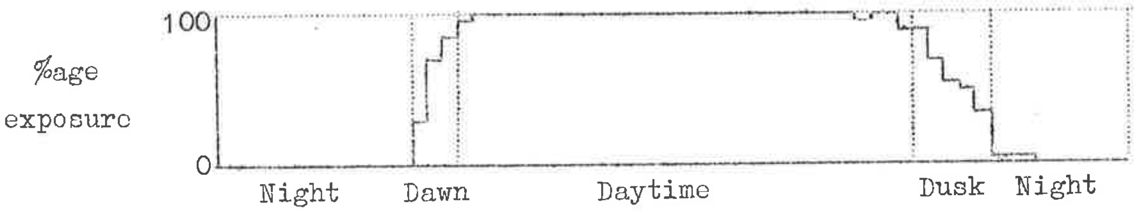
(f) Port Germein Gorge. n = 5.

(g) Telowie Gorge. n = 1.

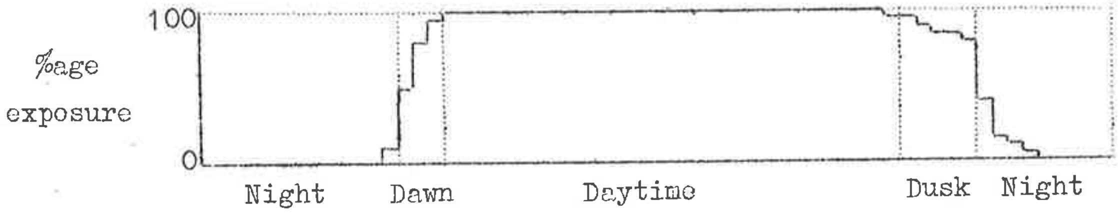


(h) Animal from Telowie Gorge tested when dehydrated.

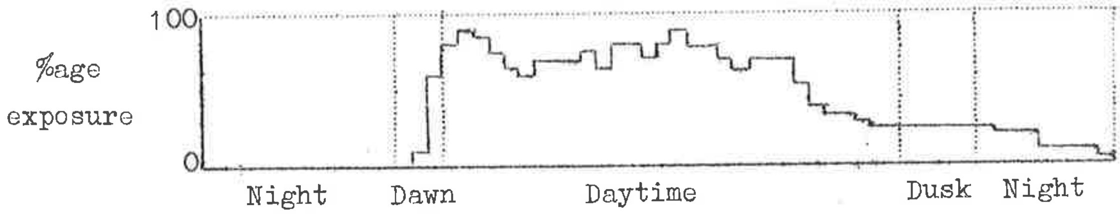
Figure 32 cont. Diurnal exposure pattern of E. m. personata in the thermal gradient regime. The animal from Port Germein Gorge shown in (e) was run for 20 days, the five animals from Port Germein Gorge were run for 5, 10, 20, 20, 30 days respectively, the animal from Telowie Gorge was run for 20 days while fully hydrated and 5 days while dehydrated. Data collected after exposure pattern had stabilised - see S4.2.3.3.



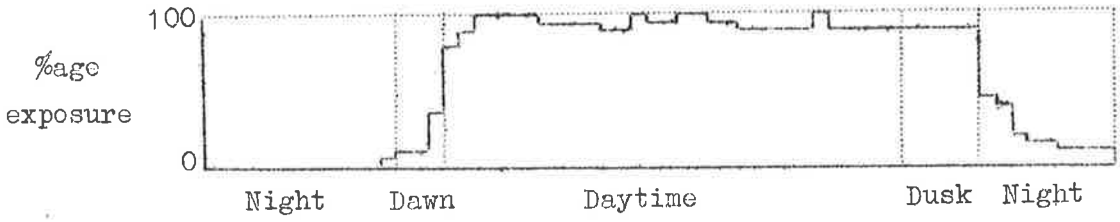
(a) Animal from St Francis Island with greatest restriction of exposure.



(b) St Francis Island. n = 3.

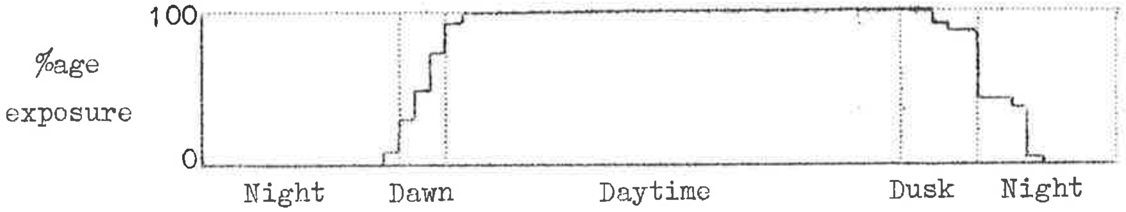


(c) Animal from Marion Bay during period of early retreat. Data collected from 19.7 - 7.8.1971.

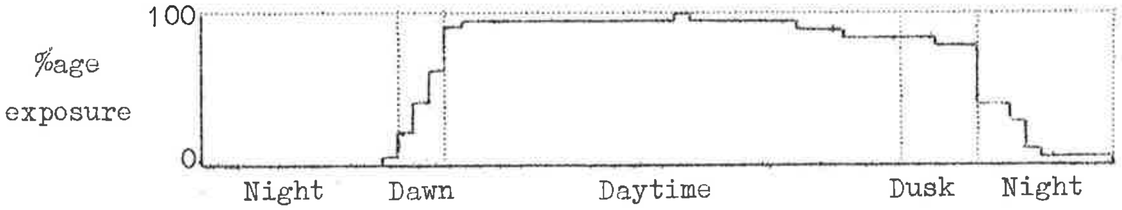


(d) Animal from Marion Bay during period of continuous exposure. Data collected from 5.7 - 6.7.1971; 13.7 - 18.7.1971; 8.8 - 19.8.1971 from the same animal as in (c).

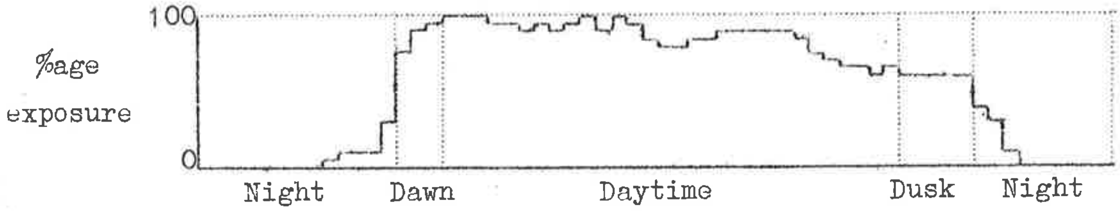
Figure 33. Diurnal exposure pattern of E. multiscutata in the thermal gradient regime. See also next page. The animal from St Francis Island shown in (a) was run for 50 days, the three animals from St Francis Island were run for 15, 18, 50 days respectively, and the results from an animal from Marion Bay shown in (c) and (d) cover 20 days each. With the exception of (c) and (d), data were collected after the exposure pattern had stabilised - see S4.2.3.3.



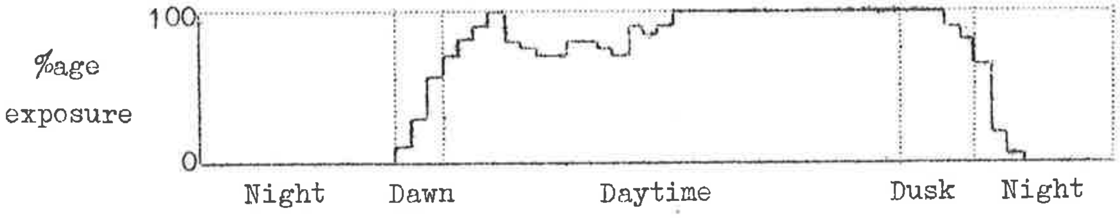
(e) Combined results from the two animals from Marion Bay showing uniformly continuous exposure.



(f) Marion Bay. n = 3.

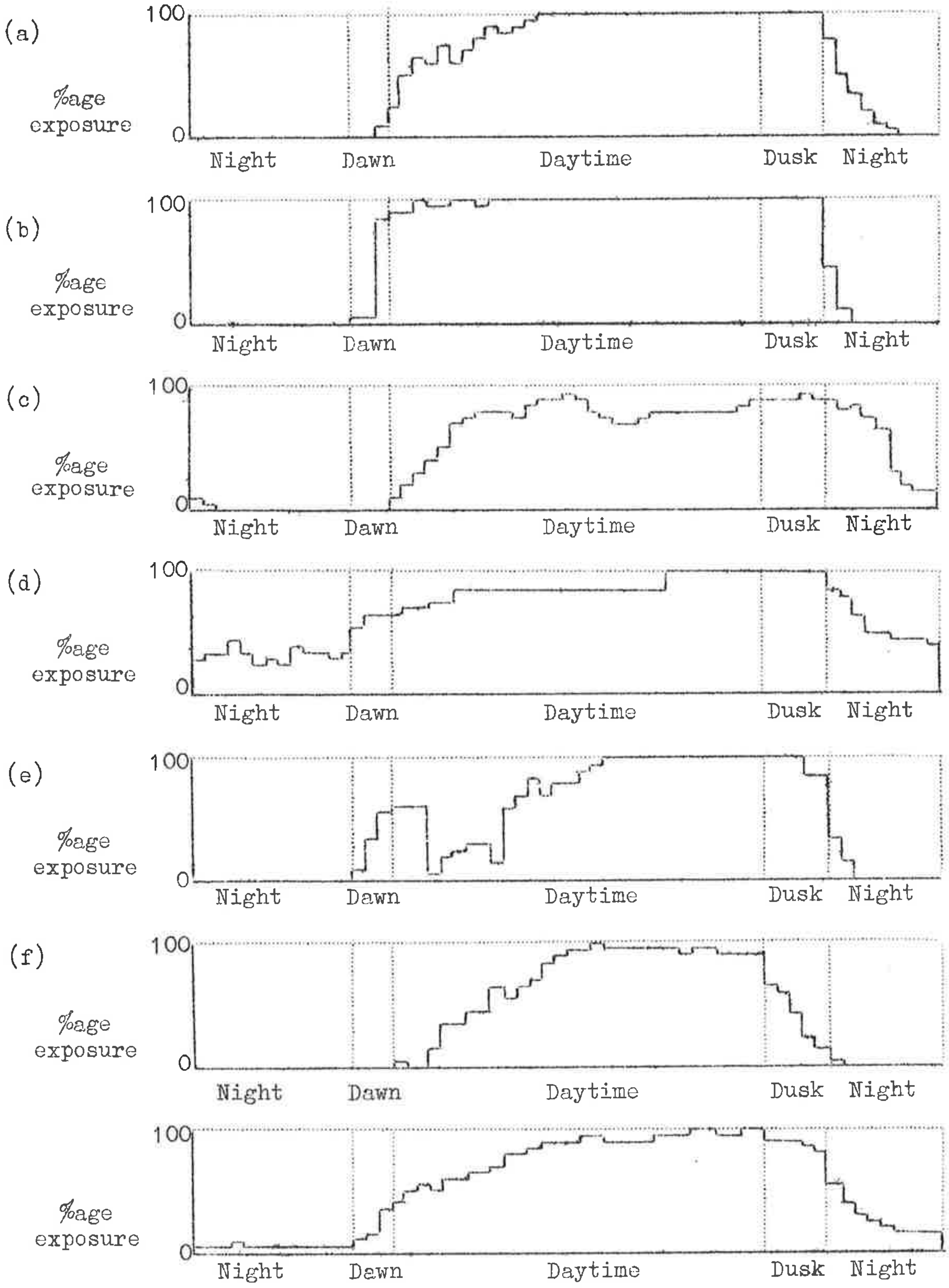


(g) Results from one of the two animals from Remarkable Rocks.



(h) Results from the other of the two animals from Remarkable Rocks.

Figure 33 cont. Diurnal exposure pattern of E. multiscutata in the thermal gradient regime. (e) shows results of two animals from Marion Bay run for 8, 15 days respectively. The three animals from Marion Bay shown in (f) were run for 8, 15, 40 days respectively. The animal shown in (g) was run for 25 days, that in (h) for 10 days. Data collected after the exposure pattern had stabilised - see S4.2.3.3.



(g) Renmark. n = 6.

Figure 34. Diurnal exposure pattern of E. inornata from Renmark in the thermal gradient regime. (a) - (f) show the results from six animals, run for 10, 10, 10, 15, 7, 15 days respectively. (g) shows the mean. Data collected after the exposure patterns had stabilised - see S4.2.3.3.

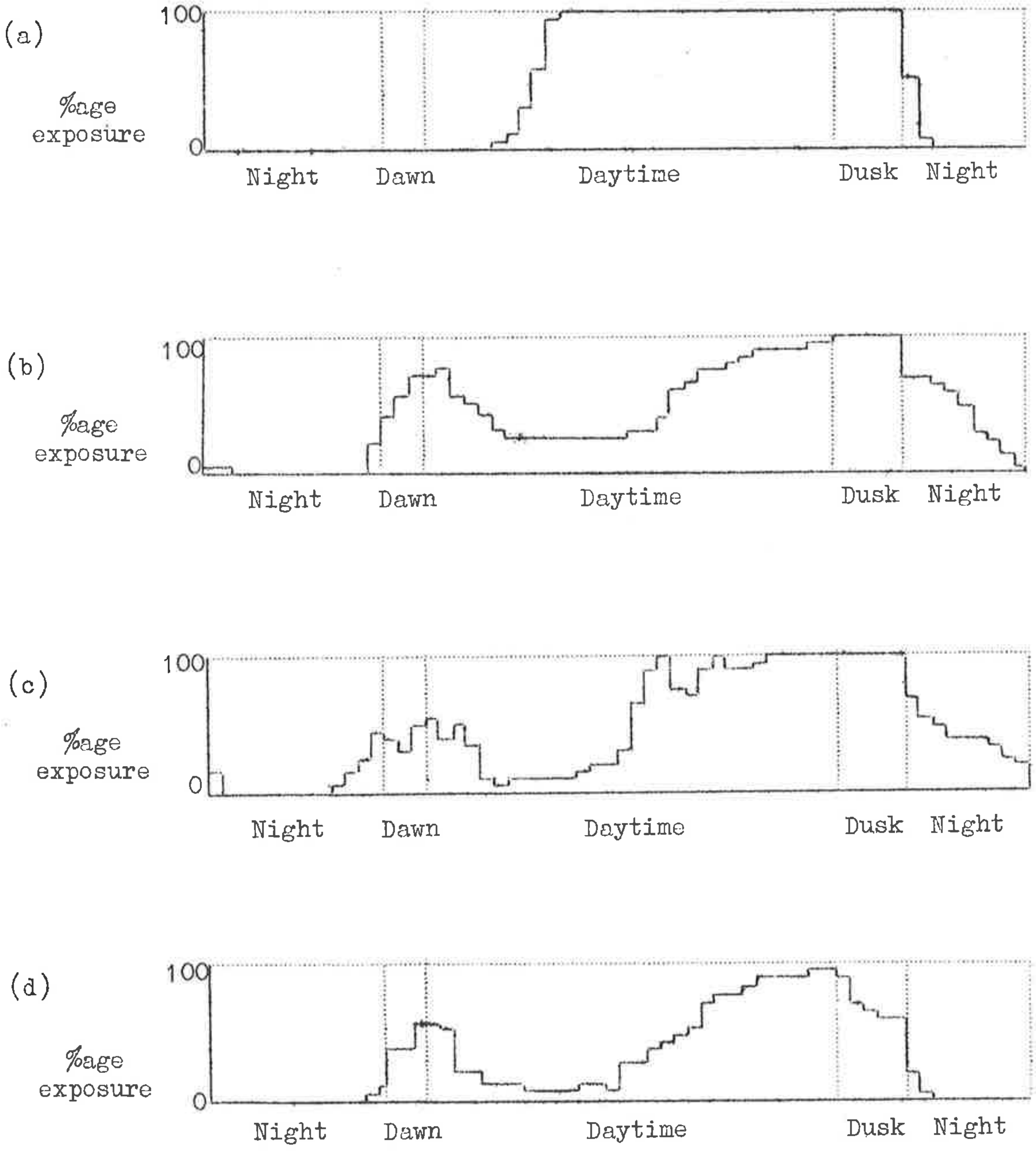
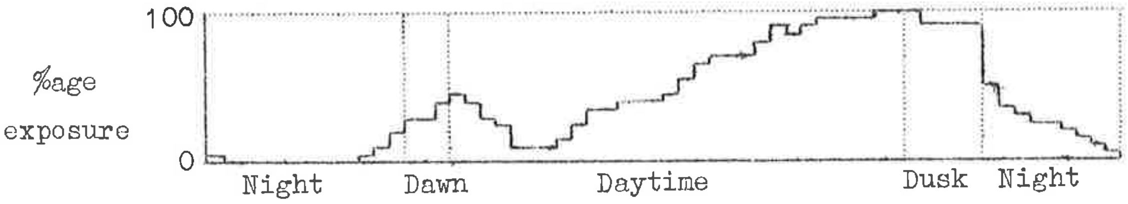
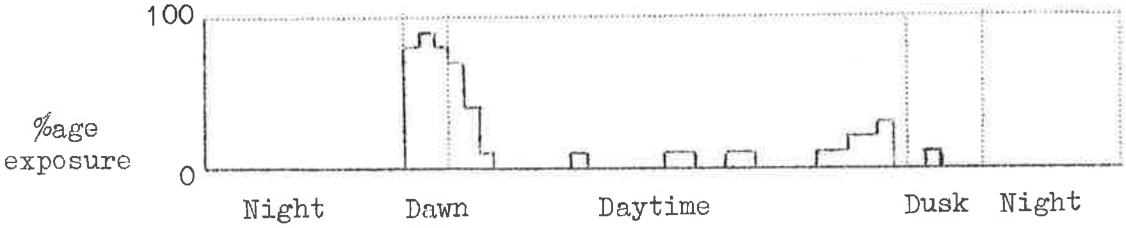


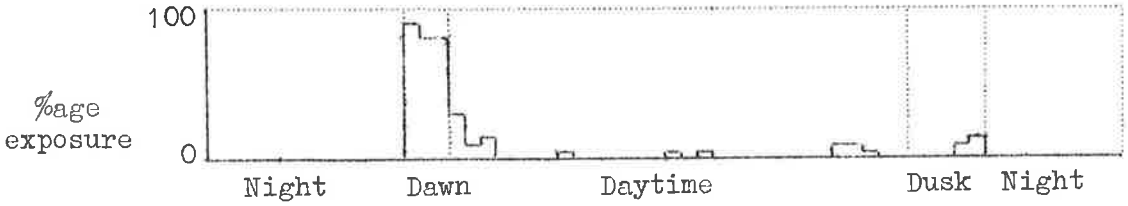
Figure 35. Diurnal exposure pattern of E. striata from Chilla Well in the thermal gradient regime. See also next page. (a) - (d) show the results from the four animals tested, measurements having been continued for 10, 20, 10, 40 days respectively after the exposure patterns had stabilised:



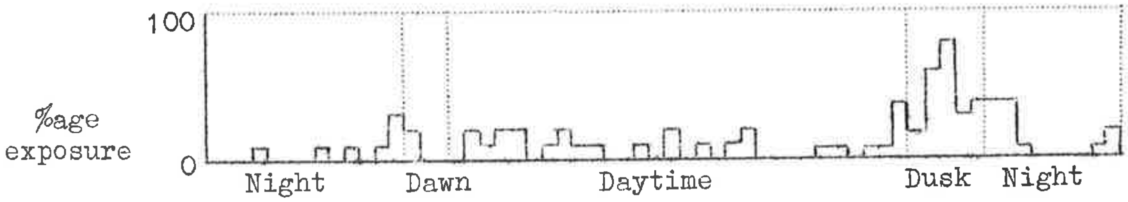
(e) Chilla Well. n = 4.



(f) Animal tested with thermal gradients inside and outside refuge.



(g) Animal tested with thermal gradients inside and outside refuge.



(h) Animal tested dehydrated.

Figure 35 cont. Diurnal exposure pattern of E. striata in the thermal gradient regime. (e) shows the mean of (a) - (d). (f) and (g) show results obtained from two animals provided with thermal gradients both inside and outside their refuges, run for 5 and 8 days respectively. (h) shows the results obtained from an animal tested dehydrated, and covers 5 days. (a), (f) were obtained from one animal and (d), (g), (h) from a second. (e), (f), (g) were obtained after the exposure patterns had stabilised.

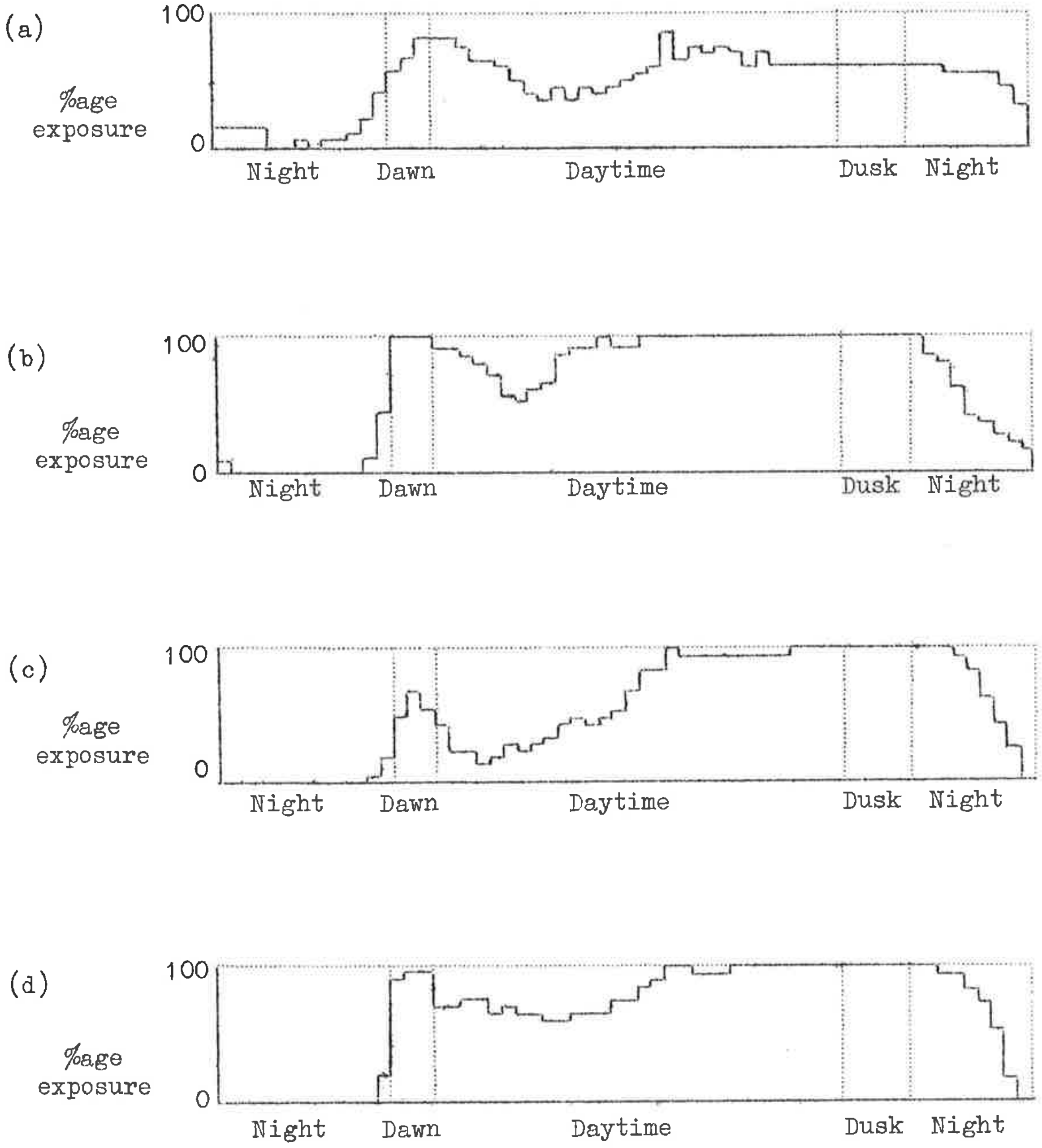
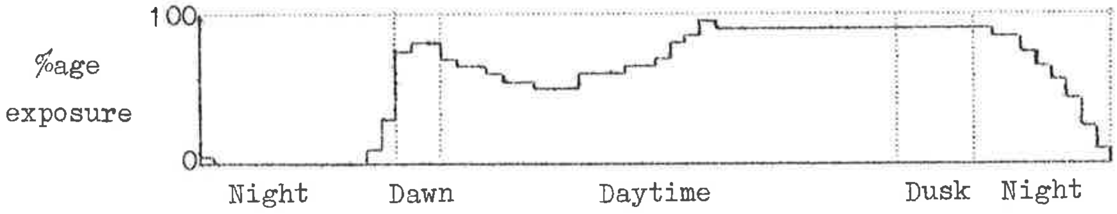
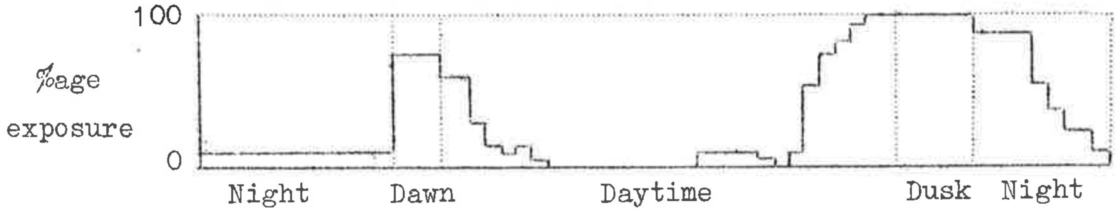


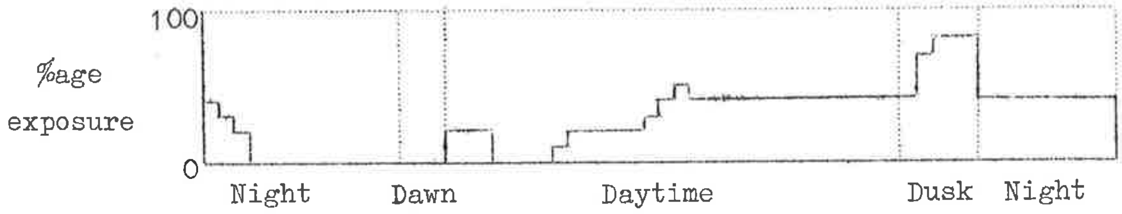
Figure 36. Diurnal exposure pattern of E. kintorei from Aileron in the thermal gradient regime. See also next page. (a) - (d) show the results from the four animals tested, measurements having been continued for for 15, 10, 15, 15 days respectively after the exposure patterns had stabilised.



(e) Aileron. n = 5.



(f) Animal tested with thermal gradients inside and outside the refuge.



(g) Animal tested dehydrated.

Figure 36 cont. Diurnal exposure pattern of *E. kintorei* in the thermal gradient regime. Animals from Aileron. (e) shows the mean of (a) - (d). (f) shows the results from an animal which had thermal gradients both inside and outside its refuge. Measurements made over 8 days. (g) shows results obtained over 5 days from a dehydrated animal. (d), (f) were obtained from one animal, (c), (g) from a second. (e), (f) were obtained after the exposure patterns had stabilised.

diurnal exposure pattern could be found. Animals would sometimes go without food for several days, or start eating during an experiment; no change in exposure pattern could be correlated with these events. Exposure on days during which the animal was known to have drunk was no different from exposure on other days, although it is possible that the lizards drank every day but that this was not detected. If an animal was deprived of water, it reduced its exposure. Extensive data were not collected, and the results are shown in Figures 32h, 35h, 36g. Additional data on the influence of water deprivation on exposure in the high temperature regime are shown in Figures 38b, 40d, 42d, 43b, d, 44b, d.

4.3.4 Diurnal exposure pattern: high temperature regime.

The diurnal exposure patterns did not appear to be influenced either by the duration of captivity or the time of year the results were obtained.

4.3.4.1 Diurnal exposure pattern of *Egernia whitei*. Three animals were tested, two from Remarkable Rocks and one from Wedge Island (see Figure 37). Two emerged intermittently, being exposed with a frequency decreasing progressively throughout the daylight hours (see Figure 37a, c); the third remained entirely within its refuge during the afternoon (see Figure 37b). The diurnal exposure patterns are similar to either Figure 25 or Figure 27.

4.3.4.2 Diurnal exposure pattern of *Egernia margaretae*. One *E. m. margaretae* was tested while fully hydrated and while water deprived. Intermittent exposure was seen in the photographic records, and the exposure patterns are shown in Figure 38; it can be seen that exposure by the dehydrated animal was greatly reduced - the animal emerged on only 7 out of 11 days for which records were obtained, and then only for short periods.

One *E. m. personata* was tested in both the first and second high temperature regimes and the results are shown in Figure 39.

The greater exposure shown in the first high temperature regime was expected, since the heat levels used were not as high as in the later high temperature regimes. Intermittent emergence was observed in the photographic records, and the shape of the exposure curve is consistent with this (see also Figure 25). However, on some days the animal did not emerge at all during the afternoon, remaining within its refuge with a body temperature about the preferred level.

4.3.4.3 Diurnal exposure pattern of *Egernia multiscutata*. Three animals were tested, two from Marion Bay and one from Remarkable Rocks, and the results are shown in Figure 40. All animals were tested in a fully hydrated condition and the animal from Remarkable Rocks was tested on two separate occasions after having been dehydrated for one week. The photographic records showed that these animals emerged intermittently. One of the individuals from Marion Bay (Figure 40a) did not expose itself at all for much of the afternoon, and its exposure during the morning was also less than expected. The animal from Remarkable Rocks (Figure 40c) showed a slight increase in exposure at the end of the afternoon; this was due to this animal resting with its tail protruding outside the refuge for three hours on one day, a phenomenon not observed in this individual at any other time. Dehydration resulted in a decrease in exposure.

4.3.4.4 Diurnal exposure pattern of *Egernia inornata*. Three animals from 50 km south of Alice Springs were tested. Intermittent exposure was seen in the photographic records, but it is evident from Figure 41 that exposure during much of the daylight hours was greatly reduced, this being especially evident during dawn and the morning. The increase in exposure just before dusk, occurring in the absence of any amelioration in environmental temperatures, shows that exposure up to this point had been reduced below that possible for an animal emerging intermittently. It was not possible to obtain body temperature records with the large thermistor leads then being used. Although it is probable that the animals were thermoregulating in their refuges during the afternoon and possibly the later part of the morning, this could not have been the case during dawn and the early morning.

4.3.4.5 Diurnal exposure pattern of *Egernia slateri*. The three animals tested were collected from 3 km south of Alice Springs. Two of the animals were tested hydrated and one of these was then dehydrated; the third animal was tested dehydrated. The results shown in Figure 42a - b were obtained in the first high temperature regime. The heat levels in this regime were low enough that an animal which retreated gradually as environmental temperatures rose remained exposed all day. Gradual retreat was seen in the photographic records, and one animal was exposed all day while the other was exposed for the whole of the day except the late afternoon. This latter animal was dehydrated and its mean body temperature was lower than that of the former, and it was forced to retreat entirely into its refuge at some point during the afternoon. The third animal (Figure 42c - d) was tested in the third high temperature regime during winter, when cold outside air permitted virtually continuous exposure for an animal which retreated gradually. The slight variation in exposure during the daytime resulted from the animal occasionally emerging intermittently. Dehydration produced a marked reduction in exposure (compare Figures 42c and 42d). Two of the three animals were continuously, or nearly continuously, exposed throughout the daylight hours and the manner of retreat of the third indicated that it would have been so too if it had been tested in a fully hydrated condition. The circumstances under which *E. slateri* were tested were such that the animals could thermoregulate while remaining exposed and the high temperature regime was functioning in the same fashion as the thermal gradient regime. It seems reasonable to conclude that *E. slateri* would be continuously exposed in the thermal gradient regime.

4.3.4.6 Diurnal exposure pattern of *Egernia striata*. Three animals from Chilla Well were used, all being tested hydrated and two dehydrated. One animal was tested in the second high temperature regime, the other two in the third. Photographic records showed that emergence was intermittent. The diurnal exposure patterns are shown in Figure 43. In a fully hydrated condition, one of the animals avoided exposure throughout almost all of the daylight hours other than dawn and dusk (Figure 43a), a second appeared to abruptly reduce its exposure around midmorning and midday (Figure 43c), while the third, to judge from the increase in exposure just before dusk (Figure 42e), had been reducing its exposure during the afternoon, and probably also during the morning from the period just after dawn when the amount of exposure dropped abruptly. Body temperature data showed that during the afternoon the animals were thermoregulating in their refuges at the levels preferred in thermal gradients, but that retreat to the refuge during the two hours after the end of dawn resulted in their body temperature falling to about 25 C. Dehydration resulted in a decrease in exposure (see Figures 43b, d).

4.3.4.7 Diurnal exposure pattern of *Egernia kintorei*. Four animals were tested, three from Aileron and one from Chilla Well. Two were tested in the second high temperature regime and two in the third; all were tested fully hydrated and two were also tested dehydrated. Photographic records showed that exposure during the daylight hours was a mixture of intermittent emergence and gradual retreat. The exposure curves, shown in Figure 44, show that exposure was voluntarily reduced during the morning and for part of the afternoon as well. This is particularly clear in Figure 44a - e but is also detectable in Figure 44f. In the early morning retreat was associated with a fall in body temperature to about 25 C, but during the late morning and afternoon body temperatures at the preferred level could be reached inside the refuge. At some point during the afternoon the level of exposure increased in all individuals, showing that exposure up to this point had been voluntarily reduced. Dehydration did not produce as marked a reduction in exposure in *E. kintorei* as in other species, but it is possible the animals had not been deprived of water long enough for any marked reduction in exposure to develop.

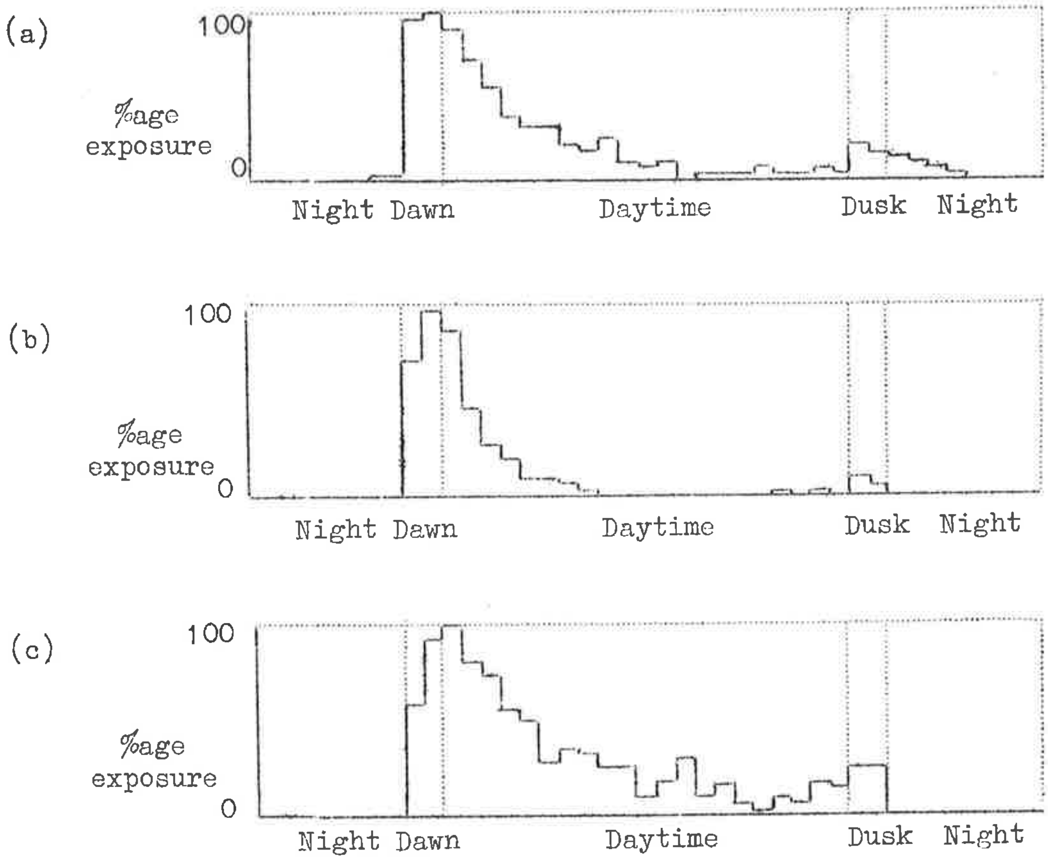


Figure 37. Diurnal exposure pattern of E. whitei in the high temperature regime. (a) is from an animal from Wedge Island tested for 9 days. (b), (c) are from two animals from Remarkable Rocks tested for 10 days each. (a) - (c) obtained in the second high temperature regime.

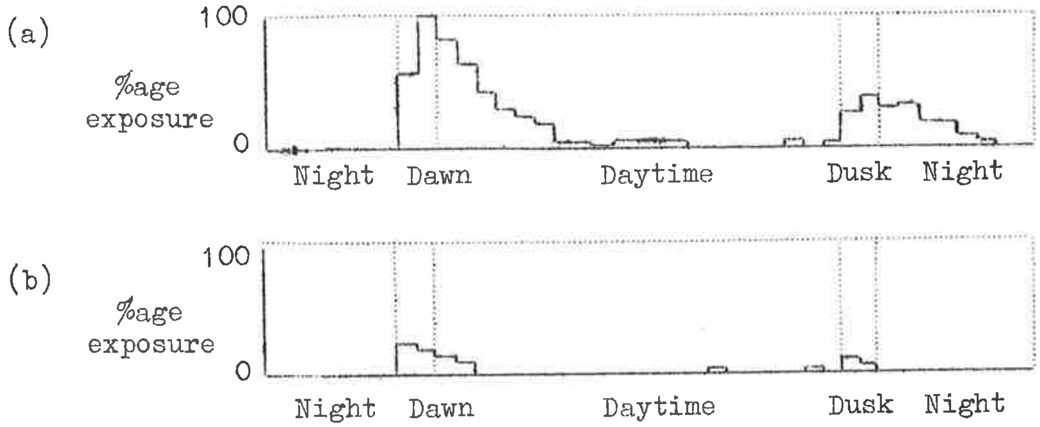


Figure 38. Diurnal exposure pattern of an E. m. margaretae in the high temperature regime. (a) The animal was run for 14 days fully hydrated. (b) The animal was run for 11 days after having been without water for 29 days before recordings were started. Both (a) and (b) were obtained in the second high temperature regime.

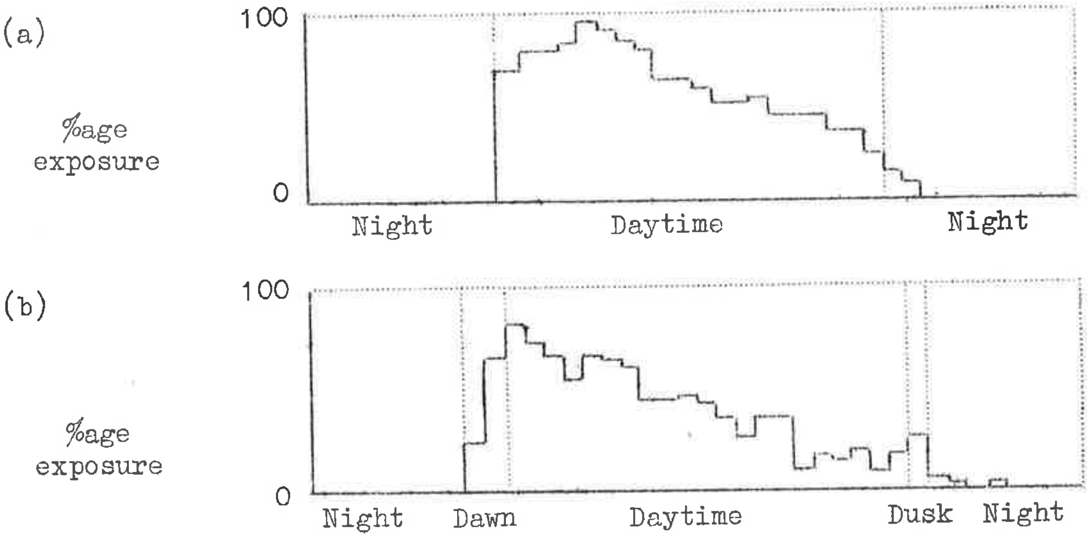


Figure 39. Diurnal exposure pattern of an E. m. personata from Wilpena in the high temperature regime. (a) Results obtained over 20 days in the first high temperature regime, (b) results obtained over 10 days in the second high temperature regime.

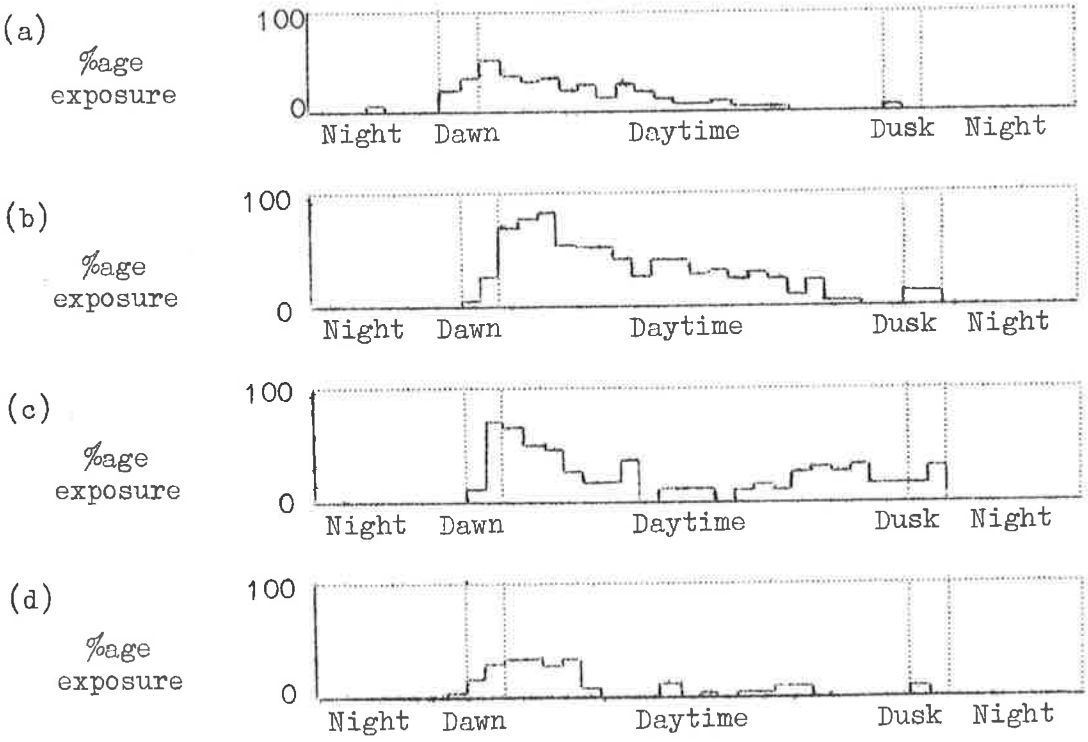
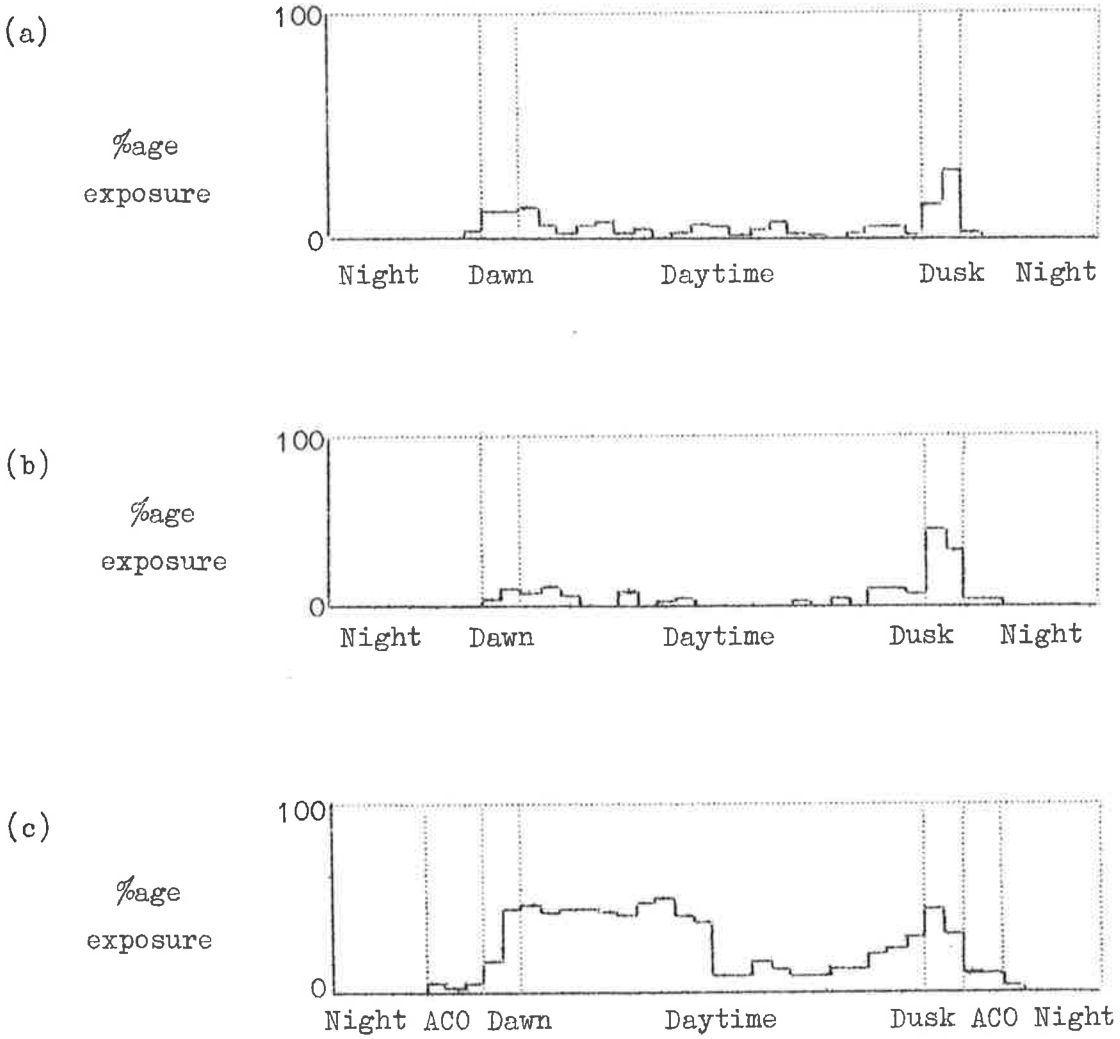
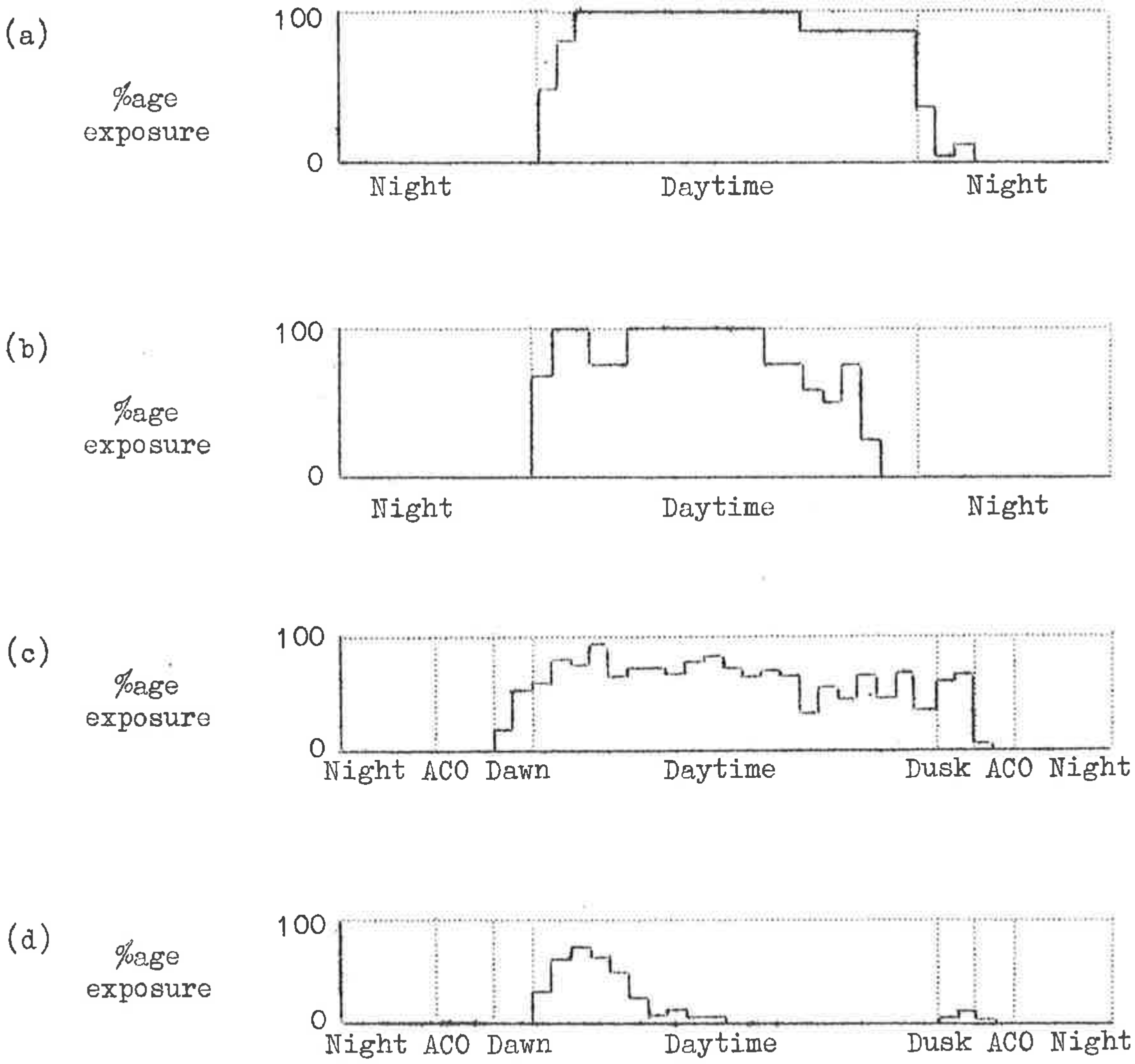


Figure 40. Diurnal exposure pattern of E. multiscutata in the second high temperature regime. (a), (b) are from two animals from Marion Bay run for 11, 9 days respectively. (c), (d) are from an animal from Remarkable Rocks: (c) fully hydrated, data collected over 6 days; (d) dehydrated, data collected over a total of 11 days on two separate occasions after the animal had been without water for 7 - 11 days.



"ACO" = air conditioner's cooling unit switched off.

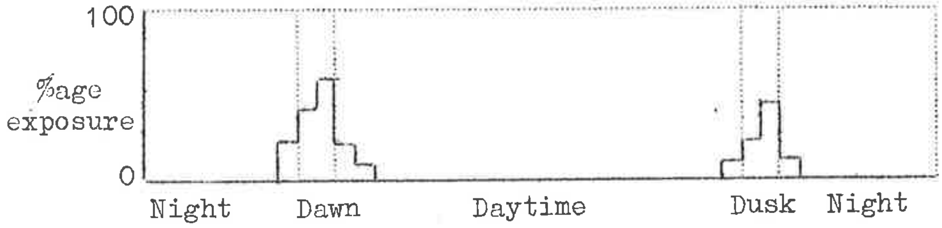
Figure 41. Diurnal exposure pattern of <u>E. inornata</u> in the high temperature regime. (a) - (c) show results from the three animals tested, for 12, 9, 15 days respectively. (a), (b) were obtained in the second high temperature regime, (c) in the third. The animals were collected near Alice Springs.



"ACO" = air conditioner's cooling unit switched off.

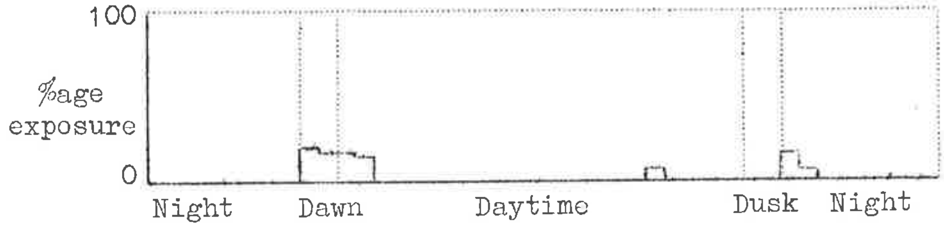
Figure 42. Diurnal exposure pattern of *E. slateri* from Alice Springs in the high temperature regime. (a) was obtained from a hydrated animal over 8 days, (b) from a dehydrated animal over 4 days. (c), (d) were obtained from a third animal, tested hydrated in (c) over 6 days and dehydrated in (d) over 6 days. (a), (b) were obtained in the first high temperature regime, (c), (d) in the second.

(a)
Animal 1,
hydrated,
2nd HTR:

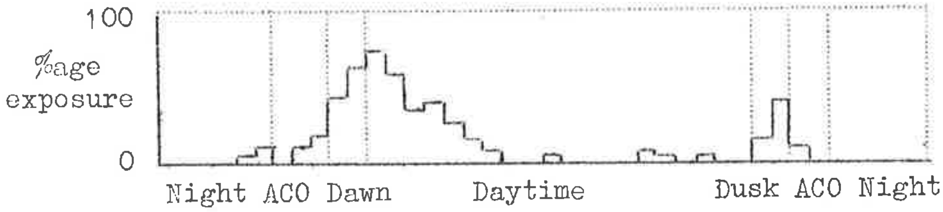


"HTR" = high temperature regime.

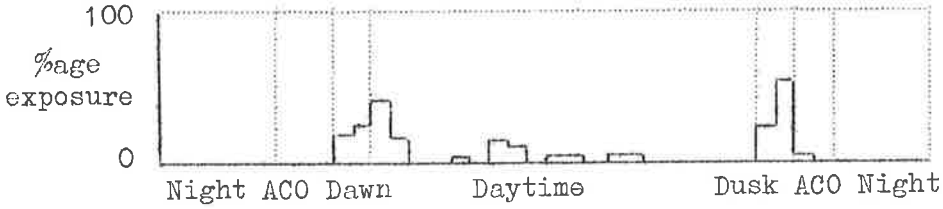
(b)
Animal 1,
dehydrated,
2nd HTR.



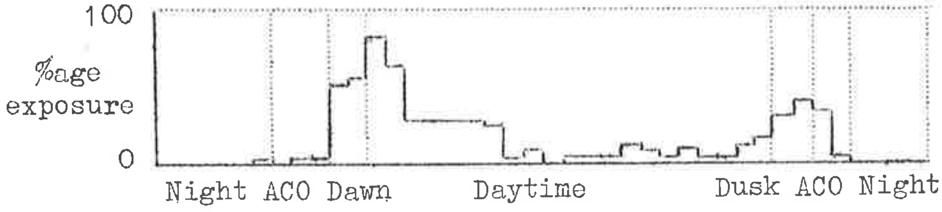
(c)
Animal 2,
hydrated,
3rd HTR.



(d)
Animal 2,
dehydrated,
3rd HTR.



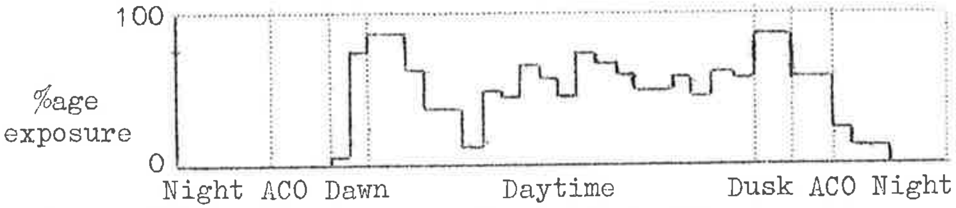
(e)
Animal 3,
hydrated,
3rd HTR.



"ACO" = air conditioner's cooling unit switched off.

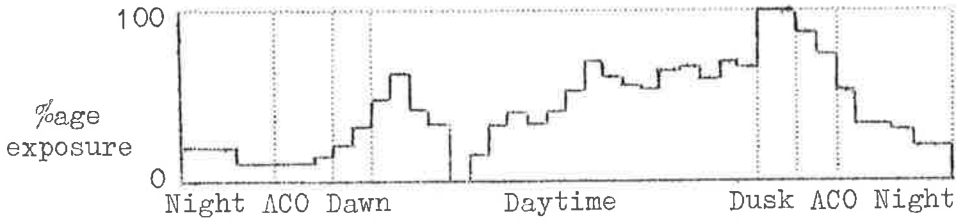
Figure 43. Diurnal exposure pattern of E. striata from Chilla Well in the high temperature regime. Three animals were tested. (a) shows results collected from one animal tested hydrated over 9 days; (b) the same animal tested dehydrated for 6 days. (c) shows results collected from a second animal tested hydrated for 8 days; (d) the same animal tested dehydrated for 8 days. (e) is from a third animal tested hydrated for 8 days. (a), (b) obtained in the second high temperature regime, (c) - (e) in the third.

(a)
Animal 1,
hydrated,
3rd HTR.



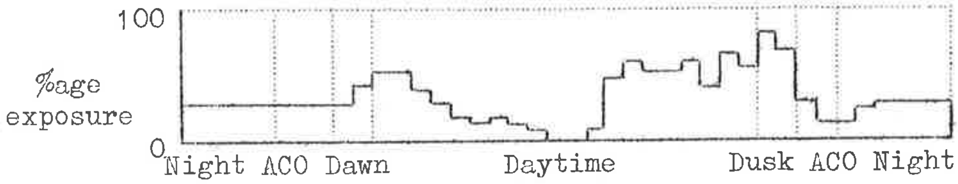
"ACO" = air conditioner's cooling unit switched off.

(b)
Animal 1,
dehydrated,
3rd HTR

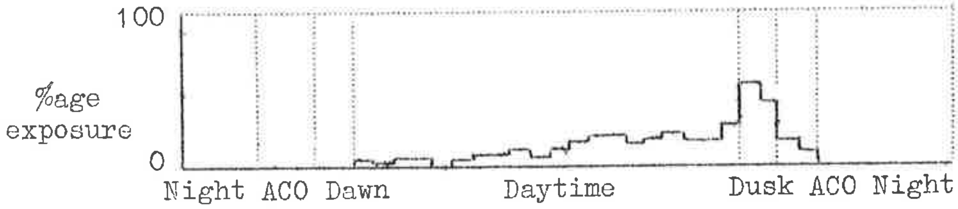


"HTR" = high temperature regime.

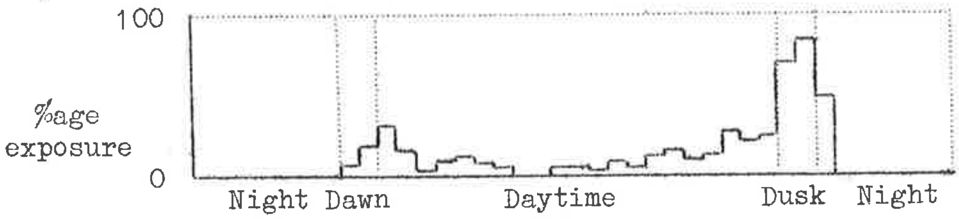
(c)
Animal 2,
hydrated,
3rd HTR



(d)
Animal 2,
dehydrated,
3rd HTR



(e)
Animal 3,
hydrated,
2nd HTR



(f)
Animal 4,
hydrated,
2nd HTR

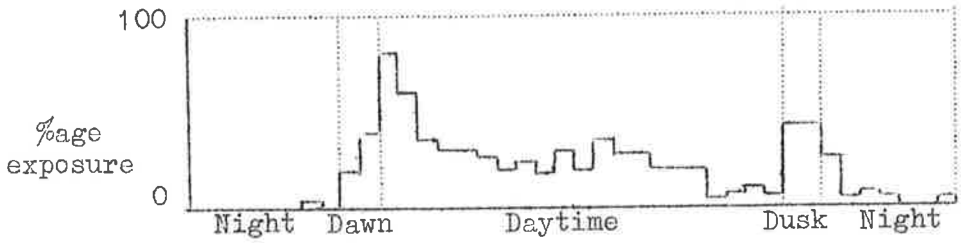


Figure 44. Diurnal exposure pattern of four E. kintorei in the high temperature regime. (a), (b) from one animal, (a) over 8 days, hydrated, (b) 9 days, dehydrated. (c), (d) from a second animal, (c) 7 days, hydrated, (d) 16 days, dehydrated. (e), (f) from two hydrated animals, over 17, 18 days respectively. (a) - (d) in third high temperature regime, (e), (f) in second. Animals shown in (a) - (e) collected at Aileron, (f) at Chilla Well.

4.3.5 Correlations between the exposure patterns obtained in the thermal gradient regime, the high temperature regime, and the field.

The diurnal exposure patterns observed during the morning for E. whitei, E. m. personata and E. multiscutata in the high temperature regime (see Figures 37, 39, 40) were similar to those predicted for animals emerging intermittently as temperatures rose (see Figure 25 or 27). Body temperature data are not available for E. whitei and E. multiscutata in the high temperature regime but measurements made on other species (including E. m. personata) indicate that during that part of the morning when thermoregulation at the preferred level was not possible within the refuge, E. whitei and E. multiscutata were exposed, and it is concluded, thermoregulating. These observations are consistent with the continuous exposure patterns shown by these species in the thermal gradient regime (see Figures 30, 32, 33). American River E. whitei showed discontinuous exposure in the thermal gradient regime, but were not tested in the high temperature regime. In some cases E. whitei and E. multiscutata did not emerge at all during the late afternoon in the high temperature regime (see Figures 37b, 40a), and it was concluded that E. whitei was thermoregulating inside its refuge in these cases. However, since in the thermal gradient regime E. multiscutata sometimes avoided exposure during the afternoon (see Figure 33c) and their body temperature fell to about 24 C, it cannot be assumed that E. multiscutata retreating during the afternoon in the high temperature regime maintained body temperatures at about 33 C inside their refuges. In the field E. whitei, E. m. personata and E. multiscutata were exposed throughout the daytime on warm days (about 20 - 28 C). On hot days (above about 28 C), E. whitei and E. m. personata were exposed during the early morning and late afternoon; I have not observed the behaviour of E. multiscutata on hot days. The thermal gradient regime can be thought of as approximating a warm day, and the high temperature regime a hot day (although in the latter case the similarity is not very precise during the late afternoon). The behaviour observed in the field is not inconsistent with that observed in the laboratory environments.

In the thermal gradient regime, most E. inornata had a low exposure during dawn and the morning, and *E. m. margaretae*, *E. striata* and *E. kintorei* avoided or reduced exposure in the morning after dawn (see Figures 31, 34 - 6). This was reflected in the high temperature regime by *E. inornata's* reduction of exposure during dawn and the morning, and in *E. striata* and *E. kintorei* by the abrupt reduction in exposure after dawn and an increase in exposure during the afternoon in *E. kintorei* (see Figures 41, 43, 44). In the single *E. m. margaretae* tested, the slight interruption of exposure during the morning seen in the thermal gradient regime was not detectable in the animal's exposure curve in the high temperature regime (see Figures 31, 38). The fall in body temperature to about 25 C (*E. striata* and *E. kintorei*) or 27 C (*E. m. margaretae*) shows that these three taxa would have emerged to a greater extent in the morning in the high temperature regime if exposure was regulated solely by thermophilia.

In the afternoon, *E. inornata* from Alice Springs increased their exposure just before and during dusk in the high temperature regime and appeared to differ from Renmark *E. inornata*, which very slightly reduced their exposure during this period in the thermal gradient regime. *E. striata*, *E. kintorei* and *E. m. margaretae* were exposed during the afternoon and dusk in the thermal gradient regime. In the high temperature regime, *E. striata* and *E. m. margaretae* were rarely, if at all, exposed during the afternoon, although exposure sometimes increased during dusk. During the afternoon, the body temperatures of *E. striata* and *E. m. margaretae* in the refuge (about 32 C) were about the same as the level preferred in a thermal gradient (about 33.5 C). It was shown for *E. striata* in the thermal gradient regime that this afternoon retreat was due to refuge-seeking, and this can be inferred for *E. m. margaretae* as well. In the high temperature regime, *E. kintorei's* exposure increased throughout the afternoon, and it was shown that in the thermal gradient regime this was due to refuge-avoiding. For *E. m. margaretae*, *E. striata* and *E. kintorei*, the exposure curves obtained in the high temperature regime are consistent with behaviour in the thermal gradient regime.

On warm days in the field, *E. slateri*, *E. inornata* and *E. m. margaretae* were visible throughout the daytime, while on hot days they emerged only during the early morning and just after sundown. This is consistent with the laboratory data, where, even though *E. inornata* and *E. m. margaretae* restricted their exposure, at least some individuals from the population should have been visible throughout the daylight hours if environmental temperatures were low enough. *E. striata* and *E. kintorei* were seen only at dusk and during the evening in the field, but not during the morning or afternoon, even on warm days. It is probable that in the field *E. striata's* burrows were warm enough on warm days for the animals to be able to thermoregulate at their preferred levels in their burrows during the afternoon, and being refuge-seeking in the laboratory during this period, would probably do so. However, in the laboratory *E. kintorei* was refuge-avoiding during the late afternoon, and would be expected to emerge in the afternoon on warm days in the field. Whether *E. striata* and *E. kintorei* emerge at dawn in the field is uncertain. The field data and the laboratory data are somewhat inconsistent. In the laboratory *E. striata* was not exposed after dusk in the high temperature regime and its exposure after dusk in the thermal gradient regime was no greater than that of *E. m. margaretae* or *E. inornata*; in the field after dusk, *E. striata* were more exposed than were *E. m. margaretae* or *E. inornata*. Also, the laboratory data indicate that *E. kintorei* should be visible throughout most of the daylight hours on warm days in the field, albeit in low numbers; Slater did not observe this. Exposure of *E. striata* and *E. kintorei* in the field would be difficult to detect unless the animals moved away from their burrows, since their burrow entrances are largely concealed by *Triodia* bushes, and it would be possible for them to emerge on warm days but to retreat before they could be seen by an approaching observer. At night both species move away from their burrows onto the adjacent sandplain and are clearly visible. The burrow entrances of all other species are clearly visible. Additional field work could show whether *E. kintorei* emerge during the daytime, and whether individual specimens of *E. m. margaretae* and *E. inornata* partially restrict their exposure during dawn and the morning.

The exposure of *E. slateri* in the high temperature regime is consistent with this species' behaviour in the field.

Exposure in the high temperature regime during dawn and the morning could be predicted quite accurately from exposure in the thermal gradient regime. However, exposure during the afternoon in the high temperature regime could not be predicted from that in the thermal gradient regime owing to the presence of an additional factor in the high temperature regime: the opportunity for animals to maintain body temperatures at their preferred level while remaining entirely within the refuge. The species differentially exploited this opportunity. When thermal gradients were provided inside the refuge as well as outside in the thermal gradient regime, exposure patterns were similar to those obtained in the high temperature regime.

In general, the data obtained in the laboratory and the field were consistent, with some minor exceptions, and exposure patterns similar to those observed in the field were obtained in the laboratory. However, much of the field data is imprecise, and it is possible that further field work would remove the presently existing inconsistencies between the two sets of data - although it might, of course, introduce additional ones.

4.4 DISCUSSION

4.4.1 Factors involved in the regulation of exposure.

Low environmental temperatures were not specifically investigated, and this account will be restricted to moderate to high temperatures. Emergence at dawn usually occurred in response to increased light levels, although some animals emerged before the lights came on, and others emerged some time after. Emergence at these times might not have occurred if environmental temperatures had been very low, such as is the case on cold days in the field. The few data available indicate that when environmental temperatures were high exposure was not prolonged by allowing the body temperature to rise above the preferred level. As environmental temperatures rose in the high temperature regime, E. slateri and some other animals positioned themselves in the shade cast by the refuges, while some other animals which emerged intermittently usually emerged partway out of their refuges. Both of these responses would reduce the heat load and prolong exposure. In neither case was body temperature elevated. The PBTs did not differ significantly among the species. Physiological regulatory devices which could possibly prolong exposure were not investigated. It is known that there are changes in blood flow through the skin of reptiles, depending on environmental conditions. These changes usually promote deep body heating if the animal is cool and its environment warmer, or retard cooling if the environment is cooler than the animal (Cowles, 1958; Bartholomew and Tucker, 1963). However, circulatory changes were considered to be of minor importance in regulating heat balance in goannas, especially at low temperatures (Bartholomew and Tucker, 1964). No experiments appear to have been performed to determine whether lizards can reduce their thermal conductances if high environmental radiation levels threaten to elevate their body temperatures above the preferred levels, and this point would be worth investigating. Dawson and Schmidt-Nielsen (1966) have shown that jack rabbits (Lepus alleni) reduce their thermal conductance at high environmental temperatures, and cite evidence to suggest that restriction of cutaneous blood flow is involved. By raising the air temperature Crawford and Kampe (1971) elevated the temperature of the lizard Sauromalus obesus to levels at which panting was induced (about 43.5 C) and found that thermal conductance was unchanged. However, since in Crawford and Kampe's work body temperatures exceeded air temperatures by 0.25 C at air temperatures of 43.5 C, the lizards were dissipating heat from the skin to the environment and would not have been expected to reduce thermal conductance even if they had been able to do so. The response might differ if air temperatures were below body temperatures and high radiation levels were elevating body temperatures above the preferred levels, since exposure would be prolonged if the animal reduced thermal conductance in those areas of skin upon which radiation was falling, but increased thermal conductance in other skin areas.

Exposure was governed by an interplay between refuge-seeking, refuge-avoiding and thermophilia. Temperate zone species were usually thermophilic and comparatively refuge-avoiding. With the exception of E. slateri, which resembled the temperate zone species, the arid zone species were thermophilic and refuge-seeking for much of the daytime. However, during the morning, refuge-seeking was strong enough to override the thermophilia, although during the afternoon E. striata, E. inornata and E. m. margaretae emerged if their refuges were not warm enough for body temperatures at the preferred level to be reached inside, indicating a dominance of thermophilia over the still present refuge-seeking. E. kintorei became refuge-avoiding during the afternoon.

Retreat at dusk usually appeared to follow the decrease in light level; some animals, especially E. kintorei, remained exposed for some hours after dusk.

4.4.2 Intraspecific variability in behaviour.

PBT data from animals from different populations of any one species are available for E. whitei, E. margaretae and E. multiscutata (see Table 15, S4.3.1.1). The data are scanty and quite variable between individuals within populations, and there is an appreciable overlap of the ranges of the PBTs of the various populations. Although more work would be required to verify this conclusion, there do not appear to be any interpopulation differences in selection of PBT.

More than one population of each of E. whitei, E. m. personata and E. multiscutata were tested in the thermal gradient regime. In E. whitei there was considerable variability in the behaviour of different populations, but little variability within any one population. Both the animals from Wedge Island were continuously exposed. Wedge Island is the most arid part of this species' range from which animals were collected. The Black Mountain population of E. whitei was also continuously exposed, but the American River population showed a reduction in exposure during the morning as large as that found in the widely distributed arid zone species. However, reduction of exposure in this population does not appear to have evolved as a response to aridity, since firstly, American River is not as arid as Wedge Island or Black Mountain, and the animals from the latter two populations are continuously exposed, and secondly the rate of water loss of *E. whitei* from American River is high (although it is possible that at American River the environment is such that *E. whitei* reduce their exposure rather than rate of water loss in order to conserve water, while at Wedge Island it has been the other way around). The interrupted exposure pattern of American River *E. whitei* appears to have evolved as a consequence of some other factor in its environment.

In *E. m. personata* and *E. multiscutata* there was a slight degree of interruption of exposure in some individuals. The three specimens of *E. m. personata* from Italowie Gorge were all continuously exposed, while only six of the 11 specimens from the other four populations showed continuous exposure. St Francis Island *E. multiscutata* were more exposed and showed less variability between individuals in exposure than animals from other parts of this species' range. Italowie Gorge and St Francis Island are the most arid parts of these species' ranges from which animals were collected, and neither species inhabits areas much more arid than these two. Although the sample sizes are small, it would appear that animals from the arid parts of these two species' ranges either do not restrict their exposure or restrict it to a lesser extent than animals from less arid areas. It is possible that populations of *E. m. personata* and *E. multiscutata* exist in which exposure is considerable restricted. None was found in the five populations of *E. m. personata* or the three populations of *E. multiscutata* sampled. If they occur, they are presumably relatively rare. Since exposure is at a maximum in the more arid parts of these two species' ranges (and in that of *E. whitei* as well), it is improbable that a population markedly restricting its exposure would occur in the arid parts of their ranges, where such an adaptation would be advantageous in water conservation. The selective pressures resulting in an increase in exposure in the more arid parts of a species' range are unknown.

In none of the arid zone species was more than one population tested in the thermal gradient regime.

4.4.3 Interspecific variability in behaviour.

There were no significant differences in PBT between the species. Other workers have measured either PBT in the laboratory or temperatures in the normal activity range in the field (Cowles and Bogert, 1944, p277 define the normal activity range as "... the thermal range extending from the resumption of ordinary routine (after the animal has ceased basking, in the case of diurnal forms) and terminates at a point just below the level at which high temperatures drive the animal to shelter."). These workers have found that there is not much variability in either PBT or normal activity range between the species of a genus, irrespective of the habitat occupied (Cowles and Bogert, 1944; Bogert 1949a, 1949b; Licht et al., 1966; Heath, 1965; Bradshaw and Main, 1968). Prieto and Whitford (1971) reported a moderate difference (3.5 C) in PBT between two species of Phrynosoma.

Many of the differences in exposure between the various species have already been mentioned in the preceding sections. These differences will now be summarised. No special effort was made in my study to determine whether or not the species differed in their innate tendencies to be exposed in cool or cold environments.

E. whitei, E. m. personata and E. multiscutata occupy only temperate or semiarid habitats and were generally similar in their exposure patterns, especially in the more arid parts of their respective ranges. In most populations all species showed continuous or near continuous exposure in the thermal gradient regime, and a relatively high level of exposure in the high temperature regime. A consistent difference was that E. whitei and E. m. personata exposed themselves more during dawn than did E. multiscutata.

There were varying degrees of restriction of exposure among the arid zone species. E. slateri behaved similarly to E. whitei etc. in showing little or no restriction of exposure if environmental temperatures were relatively low. However, E. slateri retreated gradually rather than intermittently as environmental temperatures rose, and this would result in it not being exposed at all during the afternoon if temperatures were too high for continuous exposure (it would, however, remain close to the entrance of its burrow).

E. m. margaretae showed a slight degree of interruption of exposure during the morning, but not during the afternoon in the thermal gradient regime. In the high temperature regime exposure was comparatively low during the afternoon.

E. inornata showed a substantial reduction of exposure during the morning. In the high temperature regime exposure was comparatively low during the afternoon; in the thermal gradient regime *E. inornata* were exposed for most of the afternoon. At dusk, exposure was increased by animals from Alice Springs in the high temperature regime, and reduced by one of the six animals from Renmark in the thermal gradient regime.

E. striata substantially reduced their exposure during the morning. During the afternoon, they were exposed in the thermal gradient regime, but their level of exposure was comparatively low in the high temperature regime.

E. kintorei reduced their exposure during the morning, but had a comparatively high level of exposure during the afternoon in the high temperature regime and the thermal gradient regime. *E. kintorei* remained exposed for a number of hours after dusk.

To summarise the preceding discussion of behaviour, the differences in exposure patterns observed in the field between the arid and temperate zone species appear to be a result of differences in regional diurnal temperature regimes in the case of *E. slateri* and to a combination of different diurnal temperature regimes and of innate behavioural differences in the remaining arid zone taxa.

The restriction of exposure to dehydrating conditions during dawn and/or the morning found in the laboratory in most of the arid zone members of the *Egernia whitei* species-group would result in lower overall rates of evaporative water loss in those species compared to species which did not restrict their exposure. Most summer days in central Australia are so hot that a refuge-avoiding animal would be able to emerge to a relatively small extent during the morning. The laboratory data indicate, however, that even when not exposed *E. slateri* and to a lesser extent *E. m. margaretae* would remain close to the entrances of their refuges during the morning, and would still be in a dehydrating environment compared to the cooler and moister parts of their refuges. On some days E. m. margaretae moved to cooler parts of their refuges. However, during the morning, the arid zone species markedly restricting their exposure moved to cool and probably moist parts of their refuges (E. striata and E. kintorei), or probably did so (E. inornata), and would have been in less dehydrating parts of the range of microclimates available to them.

Dehydration led to a reduction in exposure in all species. Presumably exposure would be restricted during drought, although it cannot be assumed that dehydration and drought would produce the same physiological state. Since the degree of dehydration of water deprived animals is not known in my experiments, the data cannot be analysed to determine whether some species restrict their exposure more than others in response to a given stress. Assuming that two species have the same rate of water loss, a species restricting its exposure when fully hydrated would presumably dehydrate more slowly initially. Also, one can speculate that since the degree of exposure shown by a population or species is presumably an adaptation to its environment, a population which had been selected for a high degree of exposure while animals were fully hydrated might tend to restrict their exposure less when dehydrated than animals which had restricted exposure patterns when fully hydrated.

The situation in the Egernia whitei species-group differs from that found by Bradshaw and Main (1968) in Amphibolurus and by Heath (1962, 1965) in Phrynosoma. Amphibolurus is a predominantly arid adapted group of lizards, but there are species occurring in the temperate and semiarid zones. Bradshaw and Main found that emergence occurred when specific temperature levels were reached in the animals' environments. If environmental temperatures reached high levels, exposure was prolonged both by a toleration of body temperatures above the level preferred in a thermal gradient, and by the adoption of various body postures to reduce the heat load. Light appeared to play a role only during the late afternoon, when falling temperatures induced the animals to become photophobic and to retreat.

However, all species were similar in their PBTs, and, with the exception of emergence, in the environmental temperatures at which specific thermoregulatory behaviour patterns were elicited. Species occupying cooler areas emerged at lower body and air temperatures than species from hotter environments. Exposure in the early morning would therefore be reduced in arid adapted species. The extent to which higher emergence temperatures would reduce exposure was not stated, but is probably fairly small since environmental temperature levels rise rapidly in the morning in Australian arid areas. Heatwole (1970), working on Amphibolurus inermis, one of the species studied by Bradshaw and Main, concluded that emergence (as well as retreat) "... seem to be related more to photic conditions or a biological rhythm, or both, than to temperature, since active animals in the early morning and late evening accept body temperatures lower than preferred levels at times when warmer conditions are available in the burrows.". Heatwole, however, seems to miss Bradshaw and Main's point, which is that even though emergence occurs at body temperatures below the level preferred in a thermal gradient, and might involve a short term fall in body temperatures as the animal emerges from a warm burrow, emergence nevertheless occurs at specific environmental temperatures. Heath (1962, 1965) studied the thermoregulation of various species of Phrynosoma from habitats of varying aridity. His work was conducted in the laboratory. Emergence appeared to be independent of temperature. As environmental temperatures rose, exposure was prolonged by the animals orientating the body so as to reduce the heat load, or by the animal seeking shade. These thermoregulatory behaviour patterns were elicited at higher body temperatures in the more arid adapted species than in the less arid adapted species. High temperature retreat also occurred at higher temperatures in the arid adapted species. Retreat as environmental temperatures fell was similar in all species, although mesic species possible retreated at slightly lower temperatures than did xeric species. It would appear that arid adapted species of Phrynosoma have been selected for an increase in exposure.

The three genera Egernia, Amphibolurus and Phrynosoma show a full range of changes in exposure in response to increasing aridity.

Arid zone *Egernia* species have been selected for a reduction in exposure. Adaptation to arid habitats in *Amphibolurus* has not involved major changes in the factors regulating exposure. *Phrynosoma* have been selected for an increase in exposure in arid habitats.

Only a few studies have measured exposure directly. St Girons and St Girons (1956) presented a series of figures which appear to be exposure patterns of reptiles in the field; many of these resemble the exposure patterns obtained in the high temperature regimes in my study. Minnich and Shoemaker (1970) presented diurnal exposure patterns for *Dipsosaurus dorsalis* in the field in the summer; again the results are similar to those obtained in the high temperature regimes in my study. Marcellini (1971) showed that the nocturnal gecko, *Hemidactylus frenatus*, was virtually continuously exposed from dusk to dawn in the field. Marcellini correctly pointed out that the word activity has been taken to mean two things in the literature, movement and exposure, and that confusion can arise if one tries to compare activity patterns and exposure patterns. An animal can be active while in its burrow, or resting while exposed. Although Marcellini used the word activity when exposure is what he measured, I have used the word exposure as it seems more appropriate.

5.0 GENERAL DISCUSSION

In this study, three independent types of information are available concerning the adaptation to aridity of different populations and species within the Egernia whitei species-group. These are
(1) morphology,
(2) geographical range and microhabitat selection,
(3) behaviour and physiology.

Similarity in morphology has been shown to reflect similarity in mode of life in five families of snakes by Marx and Rabb (1970) while other workers (e.g., Power, 1969; Johnston, 1969; James, 1970) have shown that intraspecific morphological variability can be attributed in part to climatic factors. Any interpretation of degrees of morphological similarity must consider the possibility of contributions by both ecology and climate to that similarity.

In his revision of the E. whitei species-group, Storr (1968) allocated six of the eight species to two sections.
(1) The E. whitei superspecies, comprising the semispecies E. whitei, E. pulchra and E. margaretae. These were stated by Storr to be dark or drab lizards with relatively long flat heads, depressed bodies and slender appendages, living among rocks or plant debris. Following Horton (1968), this section would contain four species, since Horton divided E. whitei into E. whitei and E. modesta.
(2) E. inornata, E. striata and E. kintorei are reddish or yellowish lizards with relatively short deep heads, deep bodies and short thick appendages and live in complex burrow systems in arid and semiarid regions. The remaining species, E. multiscutata and E. slateri, were stated to variously combine the characters of the two sections. E. slateri burrows in sand in the arid zone; E. multiscutata occurs in temperate and semiarid areas and in most localities burrows in sand, although it has been observed living in crevices in limestone or under granite boulders.

This broad grouping correlates partially with refuge site selection, the three rock living species grouping together and separate from the burrowing species. The problem then arises of how to account for the division within burrowing animals (the remaining species). Storr (1968) grouped three of the arid zone burrowing species together, suggesting that their similarity might derive from adaptation to arid zone conditions (e.g., possibly morphological adaptation to an existence spent predominantly in the burrow). This suggestion leaves two questions unanswered: first, although this hypothesis provides an explanation for the differences between *E. multiscutata* and *E. inornata*, *E. striata* and *E. kintorei*, it does not account for the position of *E. slateri*, also an arid zone species; and second, an explanation based on morphological adaptation to arid zone conditions in the burrowing species might be expected to lead to differences related to aridity of habitat within the *E. whitei* (temperate) - *E. m. personata* (semiarid) - *E. m. margaretae* (arid) series, differences which do not appear to exist. An alternative explanation, lacking inconsistencies and drawing upon purely morphological, biogeographical and ecological considerations, does not appear to exist.

The climates of the various areas inhabited by the respective species are classified in Table 2, S2.3.5, according to the broad divisions of Thornthwaite (1931). The microhabitats selected by each of the species have already been described. The most important features of these are that both *E. m. margaretae* and *E. slateri* would appear to exist only in areas where the relative humidity inside their burrows is high and stable, this ameliorating an environment which is otherwise arid, especially during drought. It was observed in S2.2.5 that *E. multiscutata's* burrows become deeper, have more entrances, and are located in the root system of shrubs as the area inhabited becomes more arid. That is, the location changes from warmer and probably drier parts of the range of burrow sites available to the animal in less arid areas, to cooler and probably moister parts of the range available in more arid areas. In cool areas, the emphasis seems to be on warmth for thermoregulation in and around the burrow; in more arid areas the emphasis seems to be on water conservation. It is not known whether these differences between populations in location of the burrow derive from genetic differences. Regardless of this, however, the change of burrow location in more arid areas presumably would result in a reduced rate of water loss compared to animals in burrows located elsewhere. In view of the discussion below, it is interesting that E. multiscutata's burrowing habit in the more arid parts of its range is very similar to that of E. slateri (see S2.2.7). From S2.2.6 it appears that E. inornata might resemble E. multiscutata in that burrows in the more arid parts of its range are deeper and have more entrances than burrows in less arid parts (the Simpson Desert is slightly hotter and slightly less humid than the most arid of the other localities referred to in S2.2.6). No comparative data exist for the other species. The aridity of the microhabitat occupied is, of course, the most critical test of the degree of arid adaptation of a population or species.

It was concluded earlier that there was a limit to the extent that rate of water loss could be reduced by decreasing skin permeability and respiratory water loss, and that this limit was the same for all species, with the possible exception of E. whitei. Consequently, all species have the same capacity to adapt to arid conditions by reducing standard water loss, and other reasons must be sought to account for the absence from the arid zone of certain species.

Each population can be characterised by the following figures: weight of the largest animals found, rate of water loss per unit body weight of maximum sized animals, rate of water loss of maximum sized animals, and whether exposure is continuous, restricted or extensively restricted. This data is presented in Table 23 for the population occurring in the most arid part sampled of the respective species' ranges. Although an increase in body size results in a decrease in rate of water loss per unit body weight, total water loss increases considerably. Both the smallest and the largest species in the E. whitei species-group occur in the arid zone (see Table 2), and a small or a large body size does not appear to be essential for arid adaptation. Whether a species evolves towards a large or a small body size must depend upon factors which cannot be determined on the basis of present knowledge. It is possible that a low total water loss and a low water loss relative to body weight are selectively advantageous under different circumstances, and that these circumstances have contributed to the observed variation in body size,

Table 23. Maximum attained size; rate of water loss per unit body weight, and rate of water loss, of maximum sized animals, and whether exposure is continuous, restricted or extensively restricted in the thermal gradient regime for populations from the more arid parts of the respective ranges of the species in the E. whitei species-group. Abbreviations listed below.

Species	Locality	Max size (g)	Rate of water loss (mg/g.hr)	Rate of water loss (mg/hr)	Exposure
E. whitei	Wedge Is.	21?	0.29	5.9	Continuous
E. m. personata	Italowie G.	21?	0.23	4.8	Continuous
E. m. margaretae	Reedy Creek	32?	0.19	6.2	Restricted
E. multiscutata	St Francis Is	24	0.24	5.6	Continuous
E. inornata	Alice Spr.	12	0.27	3.2	Ext. Rest.(1)
E. slateri	Alice Spr.	24	0.23	5.4	Continuous(1)
E. striata	Chilla Well	38	0.22	8.3	Ext. Rest.
E. kintorei	Aileron	180	0.14	24	Ext. Rest.

? signifies that the number of adults collected was too small to be certain that animals at or near the maximum size would have been collected.
Ext. Rest. = extensively restricted.
(1) The behaviour of E. slateri and Alice Springs E. inornata in the thermal gradient regime has been inferred from their behaviour in the high temperature regime.

possibly in conjunction with other selection pressures. Body size has played an important role at the species level in adaptation to arid habitats. However, the effect on rate of water loss of the observed variation in maximum attained size between populations within a species is comparatively small (see Table 11, S3.3.13). This suggests that size variation between populations has not been of major importance at the population level with regard to the water balance problems associated with adaptation to arid habitats. Lindsey (1966) has shown that there is no correlation between latitude and maximum attained size of a lizard species.

Marked differences between species occur in their exposure patterns. The three widely distributed arid zone species (E. inornata, *E. striata* and *E. kintorei*) all show markedly interrupted exposure patterns. The two arid zone species with restricted distributions (*E. m. margaretae* and *E. slateri*) have continuous or near continuous exposure patterns, although the data collected for these two species were not as extensive as might be desired. It was concluded that the relative humidities inside the burrows of *E. m. margaretae* and *E. slateri* are abnormally high and stable for the arid zone (S2.2.4 and S2.2.7); this would result in low rates of water loss while the animal was in its burrow. The burrows of *E. m. margaretae* and *E. slateri* are humidified by rainfall and ground water, and the latter water source would be expected to be more reliable than rainfall. Presumably the soil into which *E. inornata*, *E. striata* and *E. kintorei* burrow is humidified largely (if not entirely) by rainfall and even if the animals dug deep burrows (as do *E. striata* and *E. kintorei*) would be expected to dry out more during a drought than the refuges of *E. m. margaretae* and *E. slateri*. Since an animal with a continuous exposure pattern would be expected to have a higher rate of water loss in the field than an animal with a restricted exposure pattern, it appears that restriction of exposure is essential for survival in arid microhabitats, and that an animal lacking such restriction of exposure can persist only in temperate microhabitats within the arid zone. It is ironic that high burrow humidities are essential to animals which spend long periods of time outside, or near the entrance to, their burrows.

Some of the temperate and semiarid zone species show some restriction of exposure in the less arid parts of their ranges, but a much lesser degree of, or an absence of, restriction in the more arid parts. This is the reverse of what would be expected if the greater need to reduce rate of water loss in the more arid parts of a species' range determined the degree of exposure. It would appear that the inability of *E. whitei*, *E. multiscutata* and *E. m. personata* either to restrict their exposure to dehydrating conditions or to reduce their standard water losses below a certain level in response to increasing aridity prevents them, like *E. m. margaretae* and *E. slateri*, penetrating areas more arid than those they now inhabit.

In the E. whitei species-group the characteristic essential for persistence in arid habitats has most probably been the evolution of a reduction in exposure to dehydrating conditions in those habitats. The existence in the arid zone of two species lacking this adaptation is possible because these species are surviving in specialised microhabitats within the arid zone. It is interesting to return to the discussion on morphology, from which it was apparent that there were anomalies if it was proposed that morphology was, in part, correlated with aridity. One was that E. slateri did not group with the other arid zone burrowing species, and the other was that there were no differences among the rock living species of the same magnitude as among the sand burrowing species. Both these inconsistencies are removed if one proposes that morphologically E. m. margaretae and E. slateri are not arid adapted. Of the sand burrowing arid zone species, E. slateri was exceptional in that measurements of its rate of water loss showed little variation between animals and replicates gave similar results, while those of other species did not, and in this E. slateri resembled E. multiscutata. In the rock living taxa, rate of water loss was not reproducible in either subspecies of E. margaretae, and E. margaretae as a whole is arid adapted in this sense. The question thus does not arise as to whether E. m. margaretae can be described as being an aberrant arid zone taxon.

In a series of characters E. m. margaretae and E. slateri resemble temperate zone rather than arid zone species. This suggests that they have entered the arid zone relatively recently. Although the hypothesis presented below assumes an origin during the Pleistocene, and more particularly the Recent Period, the ancestors of E. m. margaretae and E. slateri might have been isolated prior to this, surviving the climatic fluctuations of the Pleistocene without much change. The pluvial periods of the Pleistocene provide a series of points at which the temperate adapted forebears of E. m. margaretae and E. slateri might have entered the area around Alice Springs. During the last of these pluvial periods, from about 32,000 - 10,000 years ago, cooler conditions prevailed in south eastern Australia and Tasmania. It is uncertain whether there were regional variations in the degree of cooling or whether the climate was also wetter (Galloway, 1971; Costin, 1971). If the climate ameliorated enough to allow temperate or semiarid zone species (probably *E. m. personata* and *E. multiscutata*) to colonise the areas around Alice Springs and presumably extensive areas in southern Australia, they would have occupied areas in, or close to, present day *E. m. margaretae* and *E. slateri* habitats. As aridity increased during the next 10,000 years, the ranges of *E. m. personata* and *E. multiscutata* would have contracted towards their present boundaries, the only survivors of the pluvial distributions remaining in areas offering relief from aridity. It is suggested that the habitats of *E. m. margaretae* and *E. slateri* are these areas, and that these taxa have evolved from *E. m. personata* and *E. multiscutata* respectively. This hypothesis could be tested by a number of methods, e.g., comparative serology, comparing amino acid sequences of proteins. The phylogenetic relationships of the other species are at present obscure.

A topic which will be briefly discussed is the sympatry of *E. striata* and *E. kintorei*. The two species live interspersed among one another over much of their ranges, their burrows are similar and they are similar in their body proportions. The obvious difference between the two is that *E. kintorei* is five times the mass and almost twice the length of *E. striata*. In my study a number of differences were detected between the two species which might be consequences of this size difference. The most interesting of these is that *E. kintorei* is less refuge-seeking, and hence more exposed, than *E. striata*. This increase in exposure is possibly necessary to ensure that *E. kintorei* has sufficient time to catch enough food to offset the higher total rate of water loss and also the higher total metabolic rate that would result from a larger size. However, such an increase in exposure itself intensifies the water loss problem. A field study comparing the water turnover, feeding behaviour, food preferences, and exposure of *E. striata* and *E. kintorei* should be rewarding.

One of the interesting features of the *Egernia whitei* species-group is the variability in adaptation between different populations within the species comprising it. Both rates of water loss and diurnal exposure patterns varied throughout some of the species' ranges.

Other workers have found variation in physiology between populations of a species (e.g., Lindeborg, 1952; Lee, 1963, in mammals; Dumas, 1966, in frogs; for reviews see Prosser, 1955; Vernberg, 1962), although other workers have sampled different populations and found either small differences, or no difference, between them (Roberts, 1968a, working on lizards; Kennedy and Macfarlane, 1971, working on mammals). Thus it can be a misleading oversimplification to compare the adaptations of different species to their environments by only sampling from one population of each, since a single population does not necessarily provide an estimate of the species' capacity to adapt to extreme environments. Regarding mammals, Chew (1961) emphasised the importance of studying several populations of a species. When comparing species, most workers on reptile physiology have usually used one population to represent any one species (e.g., Chew and Dammann, 1961; Bradshaw, 1965; Warburg, 1965b, 1966; Claussen, 1967; Gans _et al_., 1968; Sexton and Heatwole, 1968; Prange and Schmidt-Nielsen, 1969). Warburg (1965a) referred enigmatically to his physiological comparisons of several populations: "... but the differences found were not considered important.", and then presented combined data from two of these populations. In studies where two or more species were collected in the same area (e.g., Bogert and Cowles, 1947; Dawson _et al_., 1966; Braysher, 1972) interpretation is more complex, involves numerous possibilities, and will not be pursued here.

It is interesting to compare the adaptations to aridity of various species within each of the lizard genera _Phrynosoma_ (Heath, 1962; 1965), _Amphibolurus_ (Bradshaw, 1965, 1970, 1971; Bradshaw and Main, 1968, and Bradshaw and Shoemaker, 1967) and _Egernia_ (this study). These three investigations differed in the range of variables studied, and the comparisons, although fascinating, are incomplete. Heath's study was restricted to behaviour and was not specifically oriented towards arid adaptation; I did not study field physiology or population dynamics as did Bradshaw; neither Heath nor Bradshaw investigated variability between populations of a species.

The three genera appear to have adapted to arid habitats by quite different means. The behavioural adaptations of the three genera, summarised below, have been described in S4.4.3. Selection for arid adaptation in Phrynosoma resulted in an increase in exposure, thereby intensifying the water loss problems associated with arid habitats. To cope with the greatly increased water stress, arid adaptation must have also involved extensive changes in other parts of the animals' genotypes (e.g., relating to rate of water loss, excretion or diet). Selection for arid adaptation in Amphibolurus did not result in marked changes in the mechanisms regulating exposure. The arid zone species have presumably adapted physiologically, and Bradshaw (1965) claimed that a reduced rate of water loss in arid adapted species compensated for the more dehydrating nature of their environment; however, Bradshaw only studied one population in each species and this conclusion must be viewed with caution (see above and S3.4.2). Selection for arid adaptation in Egernia resulted in a decrease in exposure in arid adapted species. Both arid and temperate zone Egernia species have the same capacity to adapt physiologically to aridity by reducing standard water loss. Activity and excretion were not studied and diet was studied only to the point where all the species were shown to be largely insectivorous. The behavioural pattern observed in Phrynosoma resembles that occurring within the temperate and semiarid adapted species of Egernia in that there is an increase in exposure in more arid areas. It is known that the populations in the more arid parts of the temperate and semiarid zone Egernia species have lower standard water losses than other populations.

These three studies show the differences which can exist between the adaptive solutions reached by different animals to what appears to be the same environmental stress. These differences presumably originate in the different biologies of the three genera, necessitating different responses to what appears to be the same stress. The usefulness of a multivariate analysis to elucidate the process of adaptation to a particular stress is evident.

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