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Spatial ecology of a large carnivorous lizard, *Varanus varius* (Squamata: Varanidae)

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Abstract

The spatial resources used by a population of lace monitors (*Varanus varius*) were examined over an active season (September–April) and an inactive season (May–August). In total, 33 monitors were observed, of which 23 monitors were radio-tracked for up to 11 months. Radio tracking provided new information on the spatial ecology of *V. varius*. During summer (December–February), *V. varius* moved often, over large (184.5 ha) overlapping home-range areas. In the intermediate seasons of spring (September–November) and autumn (March–May), monitors moved less often and used less than 39% of the summer home-range. Finally, in the cold winter season (June–August) many monitors did not move at all and most used less than 5% of their summer home-ranges. The thermal environment, and reproductive status of *V. varius* affected its use of space, and the importance of these factors varied seasonally. No spatial segregation was noted between monitors, with home-ranges overlapping on average for eight other radio-tracked monitors. The home-range size of *V. varius* was accurately predicted using published data on body mass and home-range size for the Varanidae.

Key words: spatial ecology, *Varanus varius*, radio-tracking

INTRODUCTION

Of the many resources animals use, living space is one of the most important, providing food, water and shelter. ‘Home-range’ is the universal term for the living space of an organism and is generally defined as the area over which an animal moves during its daily activities of feeding, breeding, and shelter-seeking (Burt, 1943). Home-range sizes differ both between individuals of a species (Rose, 1982) and between species (Harris *et al.*, 1990). Factors believed to affect home-range sizes in reptiles include gender, body size, time of year, trophic level, foraging behaviour, population density, energy requirements, social behaviour and availability of mates (Turner, Jennrich & Wantaub, 1969; Rose, 1982; Mace & Harvey, 1983; Christian & Waldschmidt, 1984; Shine, 1987; Donnelly, 1989; Auffenberg, Arain & Khurshid, 1991; Secor, 1994; Stamps, 1994; Van Sluys, 1997). According to observations, the larger the animal the larger its home range (Christian & Waldschmidt, 1984); males are more active during the mating season as they search for females (Morreale, Gibbons & Congdon, 1984; Phillips, 1995); and females are less active while gravid (Carter, 1992). Although studies of home-range have become increasingly common, Christian & Tracy (1985) note that many of them have been secondary to the main objectives, with shortcomings such as small sample size and lack of knowledge about the physical and biological factors affecting use of space.

For most large varanid species, reliable information about use of space is scant, and this has resulted in general confusion about patterns of movement and spatial requirements (but see Auffenberg *et al.*, 1991; Phillips, 1995; Thompson, Boer & Pianka, 1999). The difficulties of observing these large free-ranging lizard species have led, in turn, to inadequate and biased data sets (Green & King, 1978; Thompson, 1994). Only over the past two decades have long-term, high-resolution studies of the behaviour of carnivorous lizards been possible through the development of radio-tracking techniques and devices (e.g. Auffenberg *et al.*, 1991; Phillips, 1995). Using these tools, researchers have begun to provide new insights into varanid ecology, but more information must be obtained before meaningful generalizations can be made about behaviour and ecology.

The aim of the present study was to provide a quantitative evaluation of intraspecific variation in the movements of a *Varanus varius* population living in a temperate open-savanna woodland in central western

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New South Wales, Australia. No systematic field research has been performed on inland tableland populations of this species. As a result our knowledge of the ecology and behaviour of *V. varius* in this region is limited to anecdotal observations on natural history (Stebbins & Barwick, 1968; Brooker & Wombey, 1986). The purpose of this investigation was to increase our ability to predict the detailed requirements of large lizards, by documenting their spatial requirements.

MATERIALS AND METHODS

Study species

Varanids, or monitors as they are commonly known, are powerful diurnal lizards that are characterized by an elongated muscular body, a long deeply forked tongue and a long slender snout (King & Green, 1999). The lace monitor *Varanus varius* is the second largest carnivorous predator in eastern Australia, weighing up to 14 kg and ranging in length from 0.2 to > 2 m (Weavers, 1988). Members of this species are active arboreal and terrestrial foragers and are capable of high levels of aerobic activity (Bartholomew & Tucker, 1964). Mating occurs during the late spring and six to 12 eggs are laid in termitaria (Carter, 1992). Anecdotal reports suggest that monitors have a lifespan of about *c.* 20 years (Greer, 1989).

The species is distributed along the east coast from Cape York Peninsula in Queensland to southern Victoria, and west to the New South Wales–South Australia border (Cogger, 1993).

Study site

This study was conducted at Lake Burrendong in central western New South Wales (NSW), Australia (32°40′S, 149°10′E) in topography that varies from grassland plains to steep rugged hills. The study site encompassed a wide range of microhabitats. The dry rocky slopes and ridges were covered by dense stands of *Casuarina cunninghamiana*, *Callitris glaucophylla*, *Eucalyptus sideroxylon*, *E. dealbata*, *E. blakeleyi* and *E. macrorhyncha* with canopies rarely exceeding 10 m above the ground. The upper slope woodlands were dominated by *E. albens* with an understorey of hop bush *Dodonea* spp. and sticky daisy bush *Olearia* spp. The lower slope woodlands were covered mainly by *E. albens* but also by *E. punctata*, and they tended to have a grassy understorey. Other habitats included grassy, gently sloping foreshores dominated by *Bothriochloa* spp. and *Danthonia* spp., and ephemeral creeks lined with *Angophora floribunda* and *E. melliodora*. The climate of the study area is classed as temperate.

Field protocol

Capture

Lizards were captured either with the aid of a noose and pole apparatus or in wire-mesh cage traps (1.5 m × 0.3 m × 0.4 m) baited with rabbit meat. Upon capture, lizards were transferred to hessian bags and taken to camp where they were fitted with a 1- or 2-stage radio transmitter. Two makes of 2-stage transmitters were used: ICP-1 (Biotelemetry) and Sirtrack (Scientific and Industrial Research, New Zealand). Three-quarter AA batteries powered each transmitter system. Single-stage transmitters (Sirtrack) were used for smaller individuals. The transmitter frequencies were all within the 150–151 MHz band.

Before transmitters were attached to the monitor lizards they were stitched into denim harnesses according to the methods of Green, Dryden & Dryden (1991), and waterproofed with epoxy resin. Each harness complete with its radio-transmitter had a mass in the range 10–45 g, which was < 1% of average monitor body mass. The harnesses were attached with contact cement (Selleys Gel Grip®) to the basal tail region so that the transmitter was lying longitudinally on the side of the lizard's tail, directly behind the right leg. All experimental animals were kept no longer than 24 h and were released at their respective points of capture. Radio-tracking of each animal commenced 1–2 days after release, to reduce any irregular behaviour resulting from capture.

Radio-tracking

Movements and home range were determined by analysing the locations of free-ranging *V. varius* by radio-tracking. These parameters were measured discontinuously (Harris *et al.*, 1990) for adult *V. varius* over each quarter of the year.

During this study, each *V. varius* was observed up to 4 times/day. Initial observations showed that radio-tracked monitors never moved during the night. Thus, the position of monitors was recorded up to 4 times during the active period (from 08:00 to 18:00), and at least once during the inactive period to locate roost sites.

When a monitor was located, its behaviour, surrounding habitat and the prevailing climatic conditions were noted. If the tracked lizard was active, a position near to it was marked with fluorescent tape, and once it had moved away its correct position was calculated. Locations were determined using a Magellan® GPS in conjunction with an aerial photo (1 : 5000) and an enlarged topographic map (1 : 50 000). When used alone, the GPS was accurate to within ± 1 ha, but when it was used together with the aerial photo and topographic map each fix became accurate to within ± 0.5 ha.

Analysis of locations

Movements

Displacements of monitors were recorded as the straight-line distance between successive fixes for each day. The Cartesian geometric equation below was used to determine mean distance moved per day:

$$D_I = [(X_{i+1} - X_i)^2 + (Y_{i+1} - Y_i)^2]^{\frac{1}{2}}, \qquad (1)$$

where D_I is the distance moved, (X_i, Y_i) is the first location and (X_i+1, Y_i+1) is the subsequent location (after White & Garrott, 1990).

These straight-line distances undoubtedly underestimate the actual distance moved by an animal (Laundré *et al.*, 1987; Harris *et al.*, 1990; Secor, 1994; Webb & Shine, 1997). To estimate the magnitude of this underestimation, the exact movements of 2 individual lizards were monitored with the aid of cotton spools as they moved during the day. Realized mean distances moved per active day were calculated for each monitor and compared to calculated straight-line distances.

Daily movement frequency was measured as moves/tracking day and was calculated by dividing the number of days when movement occurred (i.e. displacements > 5 m between fixes) by the number of days the animal was radio-tracked.

Home-range estimation

Minimum convex polygons (MCP) (Mohr, 1947) and kernel methods (Worton, 1987) were used to estimate home-range size. Home-range data were analysed using the radio-tracking analysis computer package RANGES V (Kenward, 1996). Both total home range and quarterly (i.e. seasonal) home ranges were calculated for each monitor.

Home-range asymptotes

Incremental area analysis (Kenward, 1996) was performed on the radio-tracking data to determine the minimum number of fixes required before the cumulative home-range size reached an asymptote (Harris *et al.*, 1990). For each home range, the fixes were randomly sorted before constructing individual incremental area curves for each range. Ranges were included in the analysis only if their incremental area curves reached an asymptote.

Statistics

Data were analysed using parametric tests outlined in Sokal & Rohlf (1995). Significance was at the 95% level or greater. Tukey–Kramer ($\alpha = 0.05$) *posthoc* tests were used for all multiple comparisons.

RESULTS

During this study, movement data were collected for 23 individual monitors: two adult females, 19 adult males and two juveniles. There were 2385 fixes in total. Nine of the 23 lizards were monitored continuously over each successive season.

Environment

As expected, patterns of environmental temperatures were highest during summer (average temperature 24 °C) and intermediate during the spring (average temperature 19 °C) and autumn (average temperature 18 °C) and lowest during winter (average temperature 10 °C).

Movement behaviour

Sightings of active radio-tracked and other non-study monitors revealed that they were largely diurnal (Fig. 1). During summer these monitors typically began their movements 1–2 h after sunrise on active days. ANOVA and Tukey–Kramer multiple comparisons revealed that mean emergence times (eastern standard time) were significantly higher in the summer 0741 ± 53 (h), than in autumn 0950 ± 40 (h), and winter 1120 ± 60 (h) (ANOVA: $F_{2,93} = 69.12$, $P < 0.001$). Once a monitor emerged from its roost site it shuttled between sunny and shady areas for about 2 h. Some animals, presumably after reaching an operating body temperature, moved from their roost sites to the surrounding terrestrial habitats; others remained based at their roost sites and continued the shuttling behaviour all day.

The hours at which lizards were active are summarized in Fig. 1. During summer, activity patterns were bimodal, i.e. the lizards were active both in the morning and in the late afternoon; they were less active in between these periods. In contrast, during autumn, winter and spring, the activity patterns of the monitors were unimodal; during these seasons 95% of the animals' relocations were observed between mid-morning and mid-afternoon. Except in winter, the seasonal figures were negatively skewed (Fig. 1). Because radio-tracking was conducted equally over all daylight hours for most working days, these trends are unlikely to reflect diurnal variations in time spent tracking or looking for either instrumented or non-instrumented monitors, respectively.

Movement distance

Individuals varied in their movement behaviour. Some travelled in a fairly unidirectional path whereas others changed direction frequently, and repeatedly stopped to look under rocks in dry creek beds, around fallen timber, within rabbit burrows and among vegetation. For two monitors, the straight-line distances between

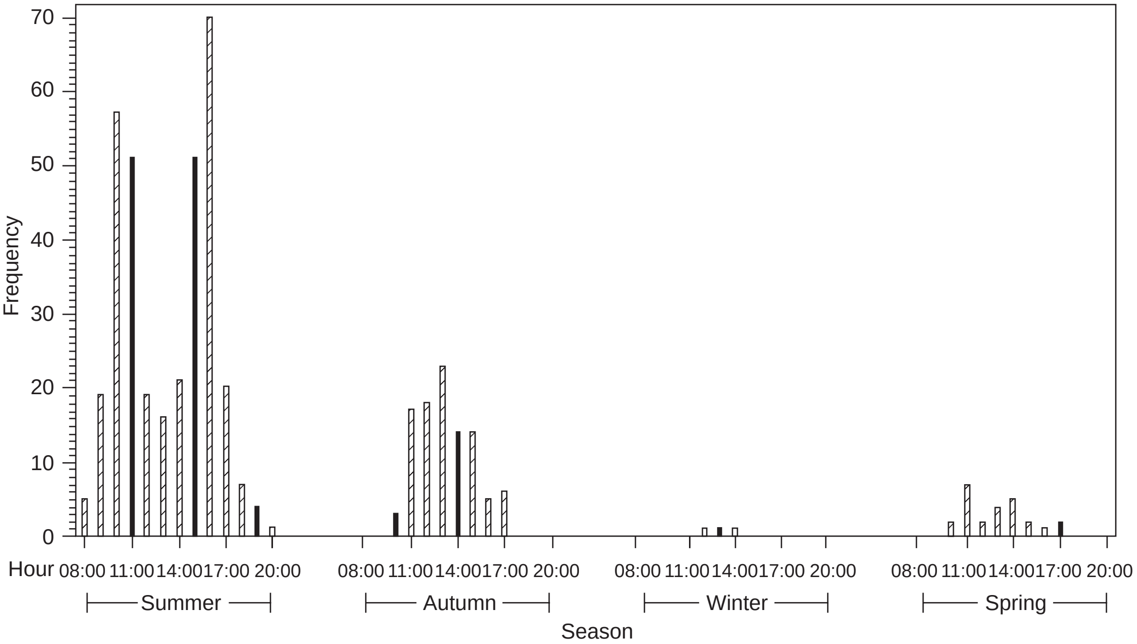

Fig. 1. Number of *Varanus varius* observed in motion at different times of the day for each season.

Table 1. Descriptive statistics (mean ± 1 SE, range, *n*) of movement parameters for *Varanus varius* compiled for each season

	Movement frequency (days of movement/days monitored)			Straight-line distance (m)		
	Mean	Range	*n*	Mean	Range	*n*
Summer	0.69 ± 0.04	0.13–1.00	19	335 ± 16	0–1800	579
Autumn	0.25 ± 0.04	0.14–0.62	13	114 ± 10	0–1350	531
Winter	0.09 ± 0.01	0.00–0.20	10	57 ± 9	0–943	92
Spring	0.48 ± 0.05	0.20–0.70	10	187 ± 33	0–1118	57

the start and stop movements were not significantly different from the actual distances travelled (paired *t*-test: $t = 0.223$, $P = 0.838$).

The mean straight-line distances monitors travelled on active days were highest during summer (335 m), intermediate during the autumn (114 m) and spring (187 m), and lowest during the winter (57 m) (Table 1). Mean daily distances moved were significantly different between seasons ($F_{3,1255} = 77.94$, $P < 0.0001$) (Table 1) and multiple comparisons revealed that the summer and winter were significantly different from one another and from the intermediary periods of spring and autumn, which were not significantly different from each other.

The longest straight-line distance travelled by a monitor on an active day occurred during the early summer and was 1800 m (Table 1). This period also coincided with the mating season. It was not uncommon for an adult monitor to move > 1000 m. Even during winter, a male monitor moved > 900 m in 1 day.

Movement frequency

Although monitors did not move every day, they usually emerged from their roost trees on most days, presumably to thermoregulate. The proportion of days for which monitors were active depended on season (Table 1) and paralleled average temperature. Movement frequency was highest during summer, intermediate during spring and autumn, and lowest during winter (Table 1). These differences were significant (ANOVA: $F_{3,47} = 25.98$, $P < 0.0001$) and multiple comparisons revealed that summer and winter movement frequencies were significantly different both from one another and from the movement frequencies in spring and autumn. Movement frequencies in the intermediate seasons were not significantly different from each other.

On sunny days during all seasons, some of the lizards were alert and active but did not leave their roost trees. For example, the largest telemetered animal (Q; Table 2) remained at the same tree for 96 consecutive days during autumn and winter. Although it frequently moved several metres to adjacent branches, it apparently never left the tree. However, on its first day of movement (during August) this male moved 1.1 km.

Home range

To determine whether monitors restricted their

Table 2. Total home ranges (100% MCP) of 23 radio-tracked monitors *Varanus varius*. SVL, snout–vent length; M, male; F, female; J, juvenile. Animals with an asterisk did not reach a home-range asymptote

Lizard no.	Sex	SVL (cm)	Mass (g)	Number of fixes	Home range (ha)	Core area (50% isopleth)
O*	J	38	900	8	4	–
7*	F	43	2300	9	11.5	4.5
2*	F	47	2790	19	39	9
C	J	53	2800	74	190	–
5*	M	58	3950	14	65.5	8
6*	M	60	4100	8	65.5	4
R	M	58	4450	117	107.5	17.5
P*	M	59	4500	38	65.5	–
T	M	66	4500	82	128	19.5
J	M	57	4550	208	132	23
K*	M	60	4850	22	377	–
F	M	61	4900	111	239	91.5
I	M	61	4900	228	387	115.5
M	M	58	4900	122	268.5	90
1*	M	62	5300	12	21.5	10.5
4	M	63	5300	232	286	134.5
H	M	63	5400	224	158	21.5
U	M	58	5800	92	183.5	42.5
L	M	61	5900	160	137	27.5
G	M	72	6000	232	345.5	82.5
9	M	60	6150	224	246	18.5
3*	M	65	6250	10	10.5	–
Q	M	64	6450	139	261.5	55.5
Grand mean		58.6	4650	104	162.2	43.1
SD		7.4	1378	87	120.7	41.5

movements to a home range, or wandered randomly, the spatial arrangement of successive locations were examined and the distance from the original release point plotted against days since release (see Slip & Shine, 1988). If monitors wandered randomly then there would be a tendency for them to be located, on average, farther and farther away from the initial release site (Slip & Shine, 1988). Based on this data-set there was no significant relationship between the distance that a monitor was located from its initial release site and the number of days since release ($F_{1,1056} = 0.072$, $P = 0.7882$, $r^2 = 0.0001$).

Further evidence that monitors occupy well-defined home ranges comes from the incremental area analysis curves. For animals with at least 60 observations these curves became asymptotic, indicating that after the plateau any additional fixes did not significantly increase the size of the area used by the animals. For asymptotic home ranges there was no relationship between number of observations and home-range size (ANOVA: $F_{1,12} = 1.34$, $P = 0.277$, $r^2 = 0.03$). Therefore, in the ensuing statistical analyses only those home ranges which were asymptotic were compared.

Home ranges of monitors are illustrated in Fig. 2. Asymptotic home ranges varied in size from 107.5 ha to 387 ha (Table 2) based on the 100% MCP method. Ranges calculated by this method did not differ in size from those calculated by the kernel method using either 100% (paired *t*-test: $t = -1.65$, $P = 0.106$) or 95% of fixes (paired *t*-test: $t = -0.70$, $P = 0.485$) (Table 3). I used convex polygon values in subsequent analyses (95%

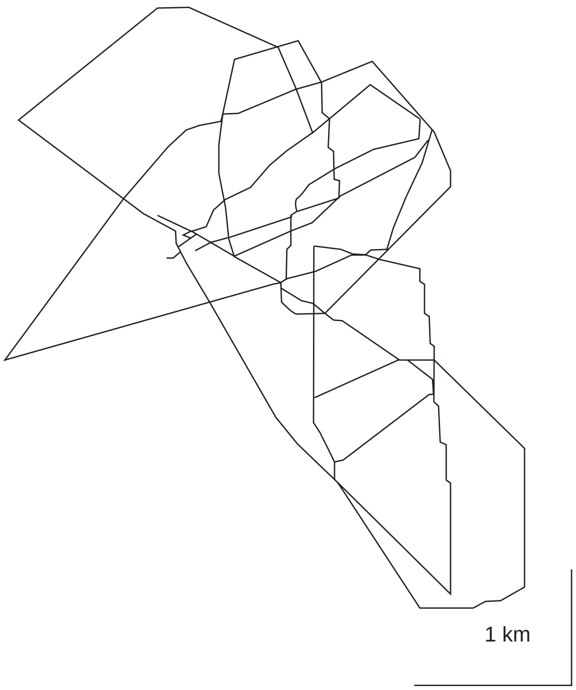

Fig. 2. Home ranges (100% MCP) of eight adult *Varanus varius* monitored with radio-telemetry. Note that the home ranges of the monitors show almost 100% overlap

Table 3. Home-range size for *Varanus varius* in each quarter of the year, according to four definitions of centre of activity (means ± SD)

	Summer (December–February)	Autumn (March–May)	Winter (June–August)	Spring (September–November)
No. of animals	12	13	10	10
No. of locations	96 ± 39	73 ± 6	33 ± 9	27 ± 9
100% MCP (ha)	184.5 ± 64	76.9 ± 74.0	10.0 ± 6.1	69.4 ± 70.4
95% MCP (ha)	159.9 ± 65.7	70.2 ± 69.8	15.1 ± 12.9	62.1 ± 59.9
100% Kernel (ha)	205.5 ± 81.3	94.2 ± 106.4	33.2 ± 44.7	80.7 ± 129.3
95% Kernel (ha)	134.9 ± 62.2	56.4 ± 66.8	26.6 ± 24.0	69.5 ± 72.2
Range span (m)	2419 ± 825	1245 ± 575	771 ± 478	1519 ± 1101

isopleths) because they provide more robust estimates of home-range size and facilitate comparisons among studies (Harris *et al.*, 1990).

Home range size increased both as $\log_{10}$ transformed snout–vent length increased ($F_{1,21} = 10.4$, $P = 0.004$, $r^2 = 0.33$) and as $\log_{10}$ transformed body mass increased ($F_{1,21} = 13.75$, $P = 0.0013$; $r^2 = 0.36$). These results show that larger, heavier-bodied monitors had larger home ranges. Core areas of activity (50% isopleths) represented on average 14.1 ± 9.6% of the total home-range (Table 2).

Seasonal home ranges differed in size among the four seasons (ANOVA: $F_{3,39} = 11.75$, $P = 0.0001$) (Table 3). Summer ranges were significantly larger than autumn, winter and spring ranges. In the spring and autumn the home ranges were not significantly different from one another, but were significantly larger than the winter ranges. Range spans (measured as the maximum diameter of home range) also differed significantly among the four seasons ($F_{3,39} = 9.62$, $P = 0.0001$). Multiple comparisons revealed that the summer range spans were significantly larger than the spring, autumn and winter range spans, which were not significantly different from one another (Table 3).

The majority of monitors shifted their activity centres northwards towards the steeply inclined hills from early autumn until winter. Monitors overwintered in these areas and shifted their activity centres back to the gentler slopes after spring emergence.

Spatial overlap of home ranges

The degree of overlap between home ranges of different individuals can give insights into the mechanisms determining use of space. If the presence of one monitor in an area has no net effect on that site's attractiveness then one might expect to see high overlap between individuals in space and time. In this study, total home ranges of monitors overlapped extensively at the study site, and, on average, home ranges overlapped those of 7.5 ± 3.9 other radio-tracked individuals (Fig. 2). Several male monitors were often found in a single roost tree, and on several occasions two or more male monitors were noted simultaneously feeding off a single carcass. Similarly there was no evidence of strong defence, by males, of adult females, and on one occasion six male monitors were observed courting one female. The observed overlap of adults of both sexes of *V. varius* further indicates that there is no mutual exclusion between individual monitors.

DISCUSSION

The data reported here document the natural temporal variability in the spatial ecology of a large varanid, and underscore the important influence of climatic factors and the probable influence of resource availability on the use of space by these large carnivorous lizards.

Individual *V. varius* moved extensively, especially during the summer, over large overlapping home ranges, and were diurnally active, and shifted their movement frequencies, distances travelled and home-range sizes seasonally with changes in ambient conditions.

Seasonal differences

This study clearly shows that the activity patterns, movement rates, daily distances travelled and home-range sizes were highest during the summer, intermediate during the spring and autumn and lowest during winter, roughly parallelling changes in weather conditions. During autumn, spring and, to a lesser extent, winter, the activity patterns of monitors were unimodal, with lizards being most active during the hottest part of the day (Fig. 1). However, on most days during winter, monitors did not emerge at all (Fig. 1). In contrast, over summer, activity patterns were bimodal. Throughout this period monitors emerged early in the morning, and were active both before and after the hottest part of the day (Fig. 1). These patterns are consistent with other studies of ectothermic vertebrates living in a variety of climatic zones including arid, tropical and temperate areas (Heatwole, 1976; Stanner & Mendelssohn, 1991; King & Green, 1999). Thus, in this respect, monitors and varanid lizards in general are similar to other reptiles in their diurnal activity patterns (Stanner & Mendelssohn, 1991; King & Green, 1999).

During summer, monitors can potentially spend a greater proportion of the day in locomotion instead of other activities such as obligatory thermoregulation and involuntary rest. Indeed during summer, monitors were observed in locomotion as early as 2 h after sunrise and as late as 30 min after sunset. This is a much greater range than in the winter and intermediate seasons (Fig. 1). Furthermore, both mean daily distances moved and home-range sizes were significantly greater during summer than in the other seasons (Table 1). Thus, during summer, monitors could potentially move over wider areas in search of food, shelter or prospective mates.

Weavers (1983) proposed a thermoregulatory model for *V. varius* living in south-eastern Australia. He showed that *V. varius* are unlikely to maintain an operating body temperature of *c.* 37 °C for > 1 h on a sunny mid-winter's day because ambient temperatures are generally too low. For summer, autumn and spring, Weavers (1983) calculated that monitors could maintain an operating temperature for 10, 5 and 4 h/day, respectively. Estimates for the amount of time that *V. varius* were observed in motion in this study are in proportion to those in Weavers' (1983) model. Overall, the direct consequences of this thermal pattern (i.e. decrease in temperature) on *V. varius*, would be a reduction in energetic requirements and a restriction on the time available to enter into locomotion. Thus, these factors were probably the causes of the smaller home ranges estimated for the winter and intermediary seasons, which are colder than the summer.

Breeding activity may have increased home-range size and daily distances moved over the summer. During the early summer, female monitors ovulate (Carter, 1991) and several pairs were observed both courting and mating throughout this period in the present study. Several male monitors were also noted on most days moving large distances (> 1000 m) during this period (Table 1). The male that moved 1800 m in 1 day was seen courting a female the following day at the previous night's roost tree. Other authors have noted similar behaviour by male varanids. Phillips (1995) reported that several of his radio-tracked male *V. albigularis* travelled > 2000 m in search of receptive females; Thompson *et al.* (1999) reported that a male *V. tristis* travelled > 890 m during the breeding period and Auffenberg (1981, 1994) noted similar behaviour by *V. komodoensis* and *V. bengalensis*. Carter (1990), Auffenberg (1994), Tsellarius & Men'shikov (1994) and Thompson *et al.* (1999) report that male *V. varius*, *V. bengalensis*, *V. griseus* and *V. tristis*, respectively, all follow scent trails of females during the courting period. Collectively, these studies indicate that breeding activity is mainly responsible for the large distances moved by males as well as for the high frequencies of movement observed during this study.

Out of the courting season some individuals suddenly moved long distances to the perimeter of their home ranges. A similar pattern has been documented in other monitor species (Auffenberg, 1981, 1994; Carter, 1992; Weavers, 1993) and land tortoises (Aguirre, Adest & Morafka, 1984). Such movements were common in this study and could not be correlated with season, body size or climatic effects. Although the magnitude of these movements changed seasonally, proportionally they were the same. In a similar study, Christian, Tracy & Porter (1984) found that Galapagos land iguanas moved over long distances (hence, increasing home-range size) during the hot season even though food was in abundance. These authors suggested that iguanids were selecting a particular food type that was, presumably, rich in nutrients, and were travelling further distances to find it. Monitors may have been moving long distances to locate carrion, a staple food during the mid–late summer period (Guarino, 2001). However, this hypothesis is speculative.

Comparisons among species

This study provides new information on the movements and home-range size of *V. varius*, much of which differs from the earlier results of Weavers (1993). In this study the mean home-range area calculated for *V. varius* using the MCP method (100% MCP) was 184.5 ha (Table 3), rather larger than that determined by the same methods in a coastal population of *V. varius* (mean 65 ha) (Weavers, 1993). In this study, the MCP method required at least 60 independent locations for each home range to reach an asymptote. According to Weaver's (1993) data, no individuals were assessed in this way and on average they were located a total of 14 times over a 3-year period. Thus, it seems likely that the home ranges reported by Weavers (1993) are underestimates.

The exceedingly large annual home ranges (mean 158 ha) calculated for *V. varius* (Table 2) in this study are similar to those of *V. albigularis* (mean 183 ha; Phillips, 1995). Phillips' (1995) study is the only other study on varanids that conducted incremental area analysis.

The present study was based on data from 23 radio-tracked monitors, each located, on average, 104 times (Table 2). Previous radio-tracking studies of monitors (excluding the study on *V. albigularis* by Phillips (1995) have usually involved far fewer animals (often a maximum of six) for a short period of time, often only 1 or 2 months. Although there is no doubt that intensive monitoring for short periods can yield valuable insights, the generality of the results is limited. The present study revealed extensive intraspecific variation in most of the attributes studied, suggesting behavioural flexibility among individual animals. For example, average asymptotic home-range size varied between 108 ha and 305 ha.

Turner *et al.* (1969) (equation 2) and Christian & Waldschmidt (1984) (equation 3) reviewed the literature on the relationship between the body mass of reptiles and their home-range size and calculated allometric regressions to explain the relationship. They proposed relationships between body weight W (g) of reptiles and their home-range area H (m^2) respectively as:

$$H = 120.9\,W^{0.66} \tag{2}$$

$$\log_{10} H = 2.35 + 0.502 \log_{10} W. \tag{3}$$

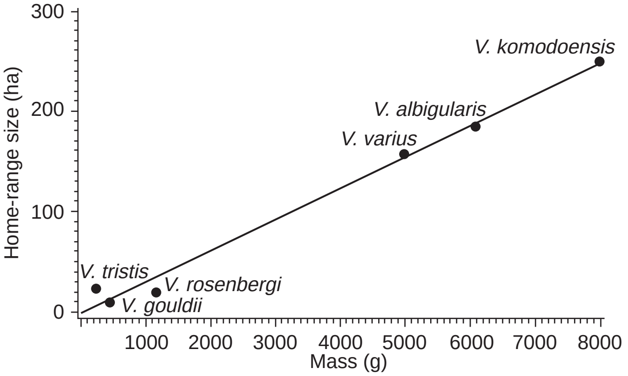

Fig. 3. Relationship between home-range size and body mass for six varanids (*Varanus gouldii*, Thompson, 1994; *V. rosenbergi*, King & Green, 1999; *V. albigularis*, Phillips, 1995; *V. varius*, this study; *V. komodoensis*, Auffenberg *et al.*, 1981; *V. tristis*, Thompson *et al.*, 1999). Values are means.

Using these expressions the predictions of home-range size for a 4.7 kg monitor are 3.21 ha and 1.56 ha, respectively, grossly underestimating the overall mean home-range size measured in this study of 162 ha. Other authors have also found that these equations result in underestimates (Green & King, 1978; Auffenberg *et al.*, 1991; Phillips, 1995; Thompson *et al.*, 1999). These discrepancies may be because Turner *et al.* (1969) and Christian & Waldschmidt (1984) derived their relationships from studies of lizards weighing no more than 210 g. Thus, investigations of relationships between body size and home range need to be revisited, with larger animals incorporated.

A relationship between varanid home-range size and body mass has been calculated using data from this and other published studies with the aim of establishing a more suitable relationship for large monitors. Home range H (ha) is related to body weight W (g) by equation (4):

$$H = 0.0307 \times W - 0.5068. \tag{4}$$

The linear relationship is significant ($F_{1,5} = 383.98$, $P < 0.0001$, $r^2 = 0.98$) and 98% of the variation in home-range size is explained by variation in body mass between species (Fig. 3).

CONCLUSIONS

Overall, factors including the thermal environment, the reproductive state of the lizards and probably food availability act in complex ways to determine the use of space by *V. varius*. The effects of, and the relationships between, these factors vary seasonally. While the thermal environment has its greatest influence on home-range size and other movement parameters during winter, it influences and is intricately connected to the daily patterns of space use during all seasons.

This study has shown that the home ranges of lace monitors are larger than those measured for other Australian varanids. It is not clear if this difference was a consequence of low sample size in other studies or habitat and resource differences between studies, but it is clear that long-term studies are required to obtain a comprehensive understanding of the area over which monitors range. The present study has also derived a new equation for predicting home-range size in the Varanidae.

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