Activity areas and daily movements of an arboreal monitor lizard, *Varanus tristis* (Squamata: Varanidae) during the breeding season

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Abstract During the breeding season, in the western Great Victoria Desert, Western Australia, male Varanus tristis move greater daily distances (186.5 m) than females (99.7 m) and have larger activity areas (40.3 ha vs 3.7 ha). V. tristis retreat predominantly to live and dead upright Eucalyptus gongylocarpa (marble gum) trees that have hollows in their trunks and limbs. There is no observable difference between males and females in their preferred habitat, but females are found more frequently in a lesser number of preferred retreats during the breeding season.

Key words: activity areas, ecology, movements, Varanus tristis.

INTRODUCTION

Rose (1982) and Christian & Waldschmidt (1984) report variations in the home range or activity area of lizards based on body mass, sex, and foraging mode. Reported home range sizes are generally underestimates of the real but unknown home range, and increase with the duration of observations (Gautestad & Mysterud 1995). Activity area, a subset of home range, is defined in this study as the area within which the lizard could be found during a defined period. Male lizards often have larger activity areas than females, and the difference may be increased during the breeding season as males actively search for females (Rose 1982). This pattern appears to be consistent for varanids.

Phillips (1995) reports reproductive-size male V. albigularis travelling significantly greater daily distances and having activity areas significantly larger than females during the two month mating period (July-August) in the Etosha National Park, Namibia. Sex differences in activity area have also been reported for other varanids. Stanner & Mendelssohn (1987) report activity areas for male V. griseus to be significantly larger than for females in the southern coastal plain of Israel. Auffenberg et al. (1991) report male V. bengalensis travel greater distances than females during wet monsoon and cool winter, and females travel greater distances during the dry and postmonsoon seasons in southern Pakistan; the activity area for males is generally larger than for females although the season was not specified. Sex differences and body mass differences were confounded in a study of activity areas of V. gouldii by Thompson (1994) with the larger males

having significantly larger activity areas than smaller females. Tsellarius et al. (1995) report activity areas for 'settled' males to be larger than for 'settled' female V. griseus.

Activity areas for predominantly arboreal or smaller species of *Varanus* are little known. Thompson (1993) provided some data on daily movements and habitat preferences for small arboreal *V. caudolineatus*, however, the study period and movement patterns did not allow inference of activity area for this species. *Varanus tristis* is an arboreal varanid from the Odatrian subgenus that is found in a variety of habitats in the northern four-fifths of Australia (Cogger 1992). Previous studies of *V. tristis* (Pianka 1971, 1982, 1994) suggest that they are most active during September and October, their mating period, although whether this activity is associated with only one sex was unclear.

Our objective was two-fold. The first was to determine if sex differences reported in sizes of activity area and daily movement patterns for other varanids during the breeding season were evident in the arboreal *V. tristis* in the western Great Victoria Desert, Western Australia. The second was to determine whether activity areas for this arboreal monitor lizard are similar to those of terrestrial species. Daily location of a number of *V. tristis* also enabled us to record additional information on how these lizards utilize their activity space, their quiescence retreats and daily linear distance travelled.

METHODS

The study site (Red Sands, 28°12'S, 123°35'E), previously used by Pianka (1994), is a complex mosaic of sand ridges and interdunal flats in the Great Victoria Desert with a vegetation of spinifex (*Triodia basedowii*),

marble gum trees (Eucalyptus gongylocarpa), Mallee trees (Eucalyptus concinna), Acacia (Acacia aneura and others) and other small bushes and grasses. This site was chosen as it enabled us to relate movement and activity area for V. tristis with information recorded during Pianka's earlier studies at this site.

Twelve *V. tristis* were captured between 11 and 29 September 1995, at the study site and given identification letters from B to M. Their dark colouration plus their geographical location indicates that they belong to the subspecies *V. tristis tristis* (Storr 1980; Cogger 1992). Each lizard was initially located and captured by following its tracks to its retreat in a hollow log, or a hollow branch of a tree.

After determining sex (everting hemipenes), weighing and measuring each lizard [snout-to-vent length (SVL) and total length (TL)], a miniature radiotransmitter from either Bio-tel, South Australia (< 10 g) or Holohil Systems, Canada (< 7 g) was either attached to the side of the base of the tail (n = 4) or surgically inserted into the abdominal cavity (n = 8). The transmitters were long and thin (~21 mm \times 12 mm \times 5 mm) and weighed less than 5% of the lizard's body mass. To insert the transmitter, the lizard was anaesthetized with isoflurane and a 30-35 mm incision was made into the lateral aspect of the lower right hand side of the abdominal wall. The transmitter was inserted through this incision into the coelomic cavity. A 27 cm hollow needle was pushed from the anterior end of the abdominal incision under the lateral skin fold to protrude near the rear of the external ear opening. The antenna of the transmitter was inserted into this needle and then the needle was withdrawn. Four or five sutures were used to close the larger abdominal incision and a single suture to close the smaller incision behind the ear. Transmitters were removed from the opposite side at the conclusion of the experiment using a reverse surgical procedure. External transmitters were sewn into a denim harness and glued to the lateral aspect of the base of the lizard's tail. The antenna ran down the tail. Monitor lizards were held overnight and released at their place of capture the next day. Surgical procedures and transmitters seemed to have little impact on lizard behaviour, as movement or activity patterns of V. tristis during the first 7 d after release did not differ from those over the subsequent 7 d and one female with an internal transmitter later laid eggs.

Each lizard was located with minimal disturbance once every day using a Biotelemetry receiver (RX3: Bio-tel, South Australia) with a 3EY directional antenna operating in the 150–151.5 MHz band. However, V. tristis often appeared to have detected our presence before their exact location was known. The location was established by triangulation based on compass bearings from the lizard's location to at least two elevated control points placed throughout the study site.

Activity area for each *V tristis* was calculated using the minimum convex polygon method (Jennrich & Turner 1969; Calhome software, US Forest Service and California Department of Fish and Game, USA) and by the determinant of the covariance matrix of the capture points (Jennrich & Turner 1969). Differences in activity areas between sexes were evaluated by ANCOVA, with body mass as the covariate.

Notes were maintained of evidence of courtship and breeding behaviour, e.g. males following scent trails, pairs together and hole digging activity. *Varanus tristis* tracks in the sand were also used to determine foraging behaviour and movement patterns between roosts.

RESULTS

We could not estimate the total number of *V. tristis* within the study area. However, tracks of other *V. tristis* were regularly noted. One individual (C) could not be located using the transmitter after 5 d, so data for this lizard have been excluded from all analyses.

Activity area

Body mass-corrected activity area varied significantly (ANCOVA: $F_{1,8} = 22.8$, P < 0.05) between males (mean 40.4 ha) and females (3.7 ha) (Table 1). Linear movements between trees and roosts meant that a lizard never used large sections of its minimum convex polygon during the study. *Varanus tristis* appeared to know the location of particular trees within their activity areas. They often moved over hundreds of metres directly to a tree refuge that they had occupied before, or they moved in a large loop to return to the same tree in which they had previously roosted.

Daily movement

Mean daily linear distance travelled was 139.2 m. There was a significant difference in average distance between body mass-corrected males (186.5 m) and females (99.7 m) (ANCOVA: $F_{1,8} = 15.5$; P < 0.01) (Table 1). The longest linear distance travelled in a day was 890 m for a male and 345 m for a female. Tracks of V. tristis indicate they move almost in a direct line from tree to tree and seldom deviate to forage. Spoor on the ground suggest that V. tristis climb each large tree encountered, descend and move to the next tree. The study period coincided with the mating season, and spoor often indicated that one V. tristis had followed another, frequently for up to 100 m. Tracks of the second V. tristis were most often on the top of those of the first lizard. Varanus tristis were never observed following each other, therefore we do not know if the V tristis laying the second spoor was directly behind the first or following a scent trail some time later. Male V. tristis moved from

Table 1. Differences between sexes for mass, snout-to-vent length, distance moved, activity areas and number of days between changing roosts for *Varanus tristis*

Item	Males	Females
Number Mass (g) SVL (mm) Number of days monitored Number of days moved Mean linear distance moved in a day (m) Longest linear distance moved in a day (m) Number of days between changing roosts Jennrich and Turner area 95% CI (ha) Minimum Convex polygon 100% CI (ha) Number of observations	5 228.2 ± 33.20 254.8 ± 11.90 47.6 ± 1.94 25.2 ± 2.96 186.5 ± 33.70 890 2.0 ± 0.22 71.4 ± 20.48 40.4 ± 13.47 234	6 248.8 ± 20.50 254.5 ± 7.20 33.2 ± 4.36 14.8 ± 3.68 99.7 ± 8.17 345 2.6 ± 0.30 9.3 ± 1.11 3.7 ± 0.77 194

Mean ± 1 SE; CI, confidence limits.

a retreat on average every 2.0 days while females moved on average every 2.6 days; the difference between sexes in days between changing roosts was not significant $(t_8 = 1.58; P = 0.15)$.

During the mating season, males spent most time in a tree hollow directly behind a female. For example, male E was found with female D on 16 of 21 occasions and with female F twice between 16 September and 6 October. Spoor around the base of the tree occupied by female F indicated another V. tristis (other than male E) had also climbed that tree twice when female F was there. Male G was found with female H on 10 of 18 occasions between 20 September and 6 October. A third V. tristis of unknown sex (not a study lizard) was seen in the same tree as male G and female H. In one day male B travelled a linear distance of 723 m, into the wind, to be found in a tree with female K; possibly having followed a scent from female K. Male B was recorded with female K twice, and was near, in an adjacent tree within 5 m of female K, on four other occasions. Spoor on the ground indicated that a V. tristis, other than male B, was in the tree with female K on three of these occasions. Male J was noted with female I once; male J was also recorded in the same dead tree with another unknown V. tristis.

This obvious association of male and female *V. tristis* was observed only between 12 September and 7 October, except for a single occurrence when male G was found with a female on 5 November. One female was recorded laying eggs on 21 October, about 20 cm below ground surface in the roots of a dead tree. Female D was seen in a hole in the ground on 13 and 14 October, female M was seen digging a hole in the ground on 24 October and female K was seen digging a hole on 26 October. Perhaps these were also associated with egg laying. Activity areas of monitored male *V. tristis* overlapped little, except for male G and male L. However, male L was smaller than the sexually mature snout-to-vent length (SVL) of 200 mm suggested by Pianka (1994) and was never found associ-

ated with a female. This lack of overlapping activity areas may have been a coincidence as other *V. tristis* of unknown sex occurred within activity areas of male B, male E, female H, male G and female I.

Most of the monitored lizards used a small number of retreats (e.g. one or two trees or hollow logs on the ground) on a regular basis. For example, female I was located in two trees 42% of the time, female K was located in two trees 66% of the time, female F was located in a single tree 70% of the time. *Varanus tristis* were located in their two most preferred retreats 46.8% of the time, with a significant difference between males (34.7%) and females (57.0%); $t_7 = 3.51$; P < 0.05).

Varanus tristis were located predominantly in live upright E. gongylocarpa (54.2%) and dead upright E. gongylocarpa (27.2%). They were found less frequently in hollow logs (11%), under bushes (4.4%), in holes in the ground (2.6%), or in the open (0.1%). Mature E. gongylocarpa often develop cavities in the centre of the trunk and in many large branches. Dead branches that break off provide access holes to internal cavities that are often quite extensive in large E. gongylocarpa. Varanus tristis most often enter these trees via these holes and then move around within the trees. These very wary monitor lizards are seldom seen in the open. We saw no evidence that they climb E. concinna or A. aneura although thickets of A. aneura occurred within most V. tristis activity areas. The perimeter of V. tristis activity areas often coincided with the boundary between clumps of E. gongylocarpa and E. concinna and tracks were rarely seen in areas of E. concinna. The wariness and vigilance of V. tristis would result in individuals seeing one of the researchers before their location was precisely known. A disturbed V. tristis, if a familiar hollow was close by, would often seek cover in the hollow upon being detected. On occasions when a hollow was not close by, V. tristis would remain motionless, often enabling the researcher to move to within a metre of its location. Their cryptic colour pattern made it exceedingly difficult to locate such

individuals either under a bush or in the leaf litter. We could detect no difference between the sexes in preferred habitat.

DISCUSSION

Activity area sizes are known for a number of large and mostly terrestrial monitor lizards (Green & King 1978; Auffenberg 1981; Stanner & Mendelssohn 1987; Auffenberg 1988; Auffenberg et al. 1991; Weavers 1993; Thompson 1994; Phillips 1995; Tsellarius et al. 1995). These data suggest that Varanus generally confine their movements over an extended period of time to a defined area: their home range. However, measured 'home range' size generally increases proportionally with the square root of sample size for birds and mammals (Gautestad & Mysterud 1995) and probably does the same for lizards. Studies on space utilized over shorter defined periods is often referred to as the 'activity area' (Thompson 1994). Where this period incorporates the breeding season it possibly represents the largest area utilized by male lizards but is often only a proportion of the entire area utilized by females over a longer period (Rose 1982; Phillips 1995). Some varanids also have preferred foraging sites within these activity areas (Thompson 1995), however, daily distances travelled vary enormously between days, seasons and individuals (Auffenberg 1981, 1988; Stanner & Mendelssohn 1987; Auffenberg et al. 1991; Thompson 1992, 1995; Phillips 1995) requiring çautious intra- and inter-specific comparisons.

Most research estimating activity area for large species of varanids exploits a radio-telemetry system to locate monitor lizards. However, the period over which studies took place, frequency of sightings during that period and methods of estimating activity area vary considerably (Green & King 1978; Auffenberg 1981, 1988, 1994; Stanner & Mendelssohn 1987; Auffenberg et al. 1991; Weavers 1993; Thompson 1994; Phillips 1995; Tsellarius et al. 1995). Probabilistic methods for estimating activity area size [(e.g. covariance matrix of capture points, Jennrich & Turner (1969)] consistently give larger estimates than other empirical estimates because they include space that lizards may never use (Waldschmidt 1979). Rose (1982) also recommends against use of probabilistic estimates because important assumptions associated with the normal distribution of sightings and randomness of locational data are seldom met. For these reasons, the minimum convex polygon method was deemed to be a better estimate of V. tristis activity area during the breeding season. However, we also report Jennrich & Turner (1969) probabilistic estimates for comparison with other studies (Table 1) but are aware of the effect of varying sample sizes (Gautestad & Mysterud 1995) when making comparisons.

Comparison of activity area with other lizards

Turner et al. (1969) proposed equations to describe the relationship between body mass of lizards and their home ranges, using lizards with a body mass of less than 210 g. More recently, Christian & Waldschmidt (1984) reported equations to represent the relationship between home range and a lizard's body mass which depend on both the sex of a lizard and its foraging mode. Because there are no standard protocols for estimating lizard activity or home range sizes, due caution must be exercized in making both intra- and inter-specific comparisons. The predicted home range, from Christian & Waldschmidt's (1984) equation, would be 0.36 ha for a 250 g male V tristis and 0.27 ha for a 230 g female. Both estimates are at least an order of magnitude smaller than the actual activity areas reported here. If we had collected data over a longer period, minimum convex polygons could have been larger (Rose 1982). Activity area size for other widely foraging terrestrial monitor lizards are generally an order of magnitude larger than for other lizards of comparable body mass (Fig. 1). The comparatively larger activity areas are probably associated with the relatively higher active metabolic rate of Varanus when compared with other similar sized large lizards (Thompson & Withers 1997)

Sex differences

Christian & Waldschmidt (1984) recognize that home range sizes are generally larger for male than female lizards. The activity areas of male V. tristis are significantly larger than those of females during the breeding season. Phillips (1995) reports that reproductive-sized male V. albigularis utilize their entire home range during the wet season and during a six week period that coincides with the period of observed matings. During the remainder of the year, male V albigularis utilize very little of their home range, and their daily movements are substantially restricted. If the behaviour of V. tristis is similar to V. albigularis this sexual difference in activity area for V. tristis could reflect a seasonal variation in movement patterns for males and females, a situation that could only be clarified by a full year of study. These differences in activity area size between sexes are similar to those reported for other monitor lizards (Stanner & Mendelssohn 1987; Auffenberg et al. 1991; Thompson 1994; J. A. Phillips pers. comm. 1997). Body mass and activity area are significantly related in males, but not in females (Fig. 2). The limited movement by females, partly due to the presence of males may account for the difference between sexes.

Auffenberg (1981, 1994) and J. A. Phillips (1995) report male *V. komodoensis*, *V. bengalensis* and *V. albigularis*, respectively, move greater distances than females, therefore we were not surprised that male *V. tristis*

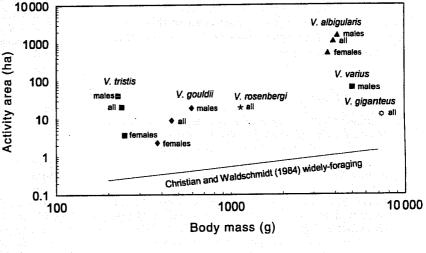
travelled further than females. The movement and location of male V. tristis appears to be dominated by the presence of females. Daily movements during the courting period could be divided into two components: movements with a female and movements to locate a female. Tasoulis (1983), Carter (1990), Auffenberg (1994), Tsellarius & Men'shikov (1994) and S. Sweet (pers. comm. 1994) report male V. varius, V. bengalensis, V. griseus and V. glauerti, respectively, follow scent trails of females. Male V. panoptes have been observed congregating in the vicinity of a large female, perhaps attracted by olfactory clues (probably pheromones: G. G. Thompson pers. obs. 1989). The smallest male (L) V. tristis was captured in the vicinity of female H, but was never recorded in a tree simultaneously with a female, although we could not be sure that a female was not present, as we had not tagged all females in the area.

The behaviour of male *V. tristis* in limiting the movement of females by placing themselves in the exit is a possible reason for the significantly higher proportion of time females spend in their two most preferred roosts. The difference in the frequency of changing

roosts between males and females probably reflects the behaviour of males monitoring the location of more than one female. Both sexes regularly returned to trees that they had roosted in previously, suggesting that they have good spatial memories. Auffenberg (1981, 1994) and Thompson (1995) report *V. komodoensis*, *V. bengalensis* and *V. gouldii*, respectively, being able to return to areas that they had previously foraged. Monitor lizards probably use both olfactory and visual cues to navigate around their activity areas. There were no detectable differences in the number or nature of retreats used by male and female *V. tristis*.

Pianka (1994) reports *V. tristis* to consume predominantly lizards (agamids, geckos and various species of *Ctenotus* skinks) and insects (grasshoppers). Prey items in stomach contents of *V. tristis* are predominantly of terrestrial origin. Tracks of *V. tristis* indicate they move almost in a direct line from tree to tree and seldom deviate to forage during the breeding season. This would suggest that *V. tristis* either are not eating or not foraging on the ground during the breeding season. Stomach contents of 52 of 63 *V. tristis* caught previously

Fig. 1. Relationship between body mass and activity area size for Varanus (V. gouldii Thompson 1994; V. rosenbergi Green & King 1978; V. albigularis J. A. Phillips pers. comm. from 1995 data; V. varius Weavers 1993; V. giganteus King et al. 1989) and a comparison with home range sizes for other similar sized lizards.



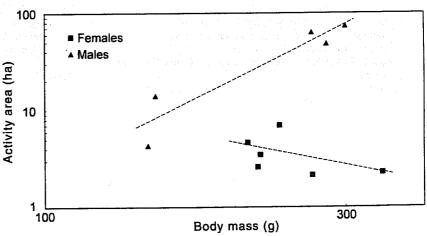


Fig. 2. Allometric relationship of activity area size for *Varanus tristis*.

in the vicinity of the study site between September and November (E. R. Pianka unpubl. data) had food items in their stomach indicating that they are eating. This would suggest that these primarily arboreal monitors are probably ambush predators that change their perches regularly. Stomachs of both male and female *V. tristis* contained prey items during the period September to November.

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