Ontogenetic differences in the spatial ecology of immature Komodo dragons

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Abstract

The early life-history stages of reptiles are extremely important to an individual's fitness, but in an ecological sense, among the most difficult to observe. Here, we used radio-tracking techniques to describe the differences in movement patterns, habitat use and home range between hatchling and juvenile Komodo dragons *Varanus komodoensis* on Komodo Island, Indonesia. The movement of hatchlings from their nests was largely linear and suggested a natal dispersal event. The movement patterns of juvenile Komodo dragons exhibited a greater spatial overlap than hatchlings, indicating greater site fidelity and thus use of a more defined activity area. The rates of daily movement were significantly less for hatchlings compared with juvenile dragons. The activity areas of hatchlings were significantly smaller than juvenile dragons. Both age classes preferred utilizing dry monsoon forest compared with other habitat types. Hatchlings were predominantly arboreal compared with juveniles and the degree of arboreal activity was strongly correlated with an individual's size. These distinct differences in spatial ecology between immature life-history stages suggest that different selection pressures may affect different size classes of Komodo dragons.

Introduction

Ontogenetic transitions through an animal's life history are often associated with large changes in their ecology (Stamps, 1983; Calder, 1984; Polis, 1984). This is particularly evident in reptiles that may vary in mass by several orders of magnitude over their lifespan and coincide with large transitions in diet, habitat use and home range (Stamps, 1983; Shine, 2005; Herrel *et al*., 2006). The most dynamic changes within an individual's life history often occur in the early life phases (e.g. post-natal and juvenile), often reflecting greater selection pressures on survival. For example, early post-natal movement, generally associated with periods of dispersal in reptiles, can range from relatively passive movements, resulting in high natal fidelity (e.g. Prickly forest skink, *Gnypetoscincus queenslandiae*, Sumner, 2006), to highly irruptive movements (e.g. marine turtles) that disperse offspring a considerable distance from their natal site (Wyneken & Salmon, 1992). Similarly, shifts in habitat use (e.g. terrestrial vs. arboreal) are often pronounced in early periods of development and again may result from multiple selection pressures acting on an individual, including food availability, morphological constraints, microclimate, predator avoidance and intraspecific aggression (Stamps, 1983; Huey, 1991).

Despite being among the most dynamic phases in the life history of reptiles, documentation of the ecological aspects of these early life stages is often constrained by a reduced capture probability (i.e. linked to small size, cryptic behavior, arboreality, wariness or reduced survival) that limits the collection of detailed ecological information at least via mark–recapture methods (Fitzgerald, Shine & Lemckert, 2002). However, squamate reptiles such as boid snakes and many varanid lizards, with their large offspring, are amenable for use with radio-telemetry techniques, allowing gathering of more detailed information on the ecological habits of early life stages (Wilson, Heinsohn & Legge, 2006). In this study, we investigated both hatchling and juvenile Komodo dragons *Varanus komodoensis* with respect to aspects of their spatial ecology and habitat requirements, which, unlike their older conspecifics, are poorly documented (Ciofi *et al*., 2007). The Komodo dragon, a large monitor lizard (up to 87 kg), is endemic to five islands in Eastern Indonesia, where it occupies a niche as a top carnivore (Auffenberg, 1981). Previous research on the spatial ecology on Komodo dragons has focused on preliminary descriptions of movements and activity area of individuals using footprint locations and sighting records Auffenberg (1981). More recently, Ciofi *et al*. (2007) estimated activity areas and the movements on five adult Komodo dragons with a

snout–vent length (SVL) of 116–154 cm. Similar studies on other varanid species have also described aspects of spatial ecology (e.g. King & Green, 1999; Thompson, De Boer & Pianka, 1999; Guarino, 2002; Ibrahim, 2002) and interactions with physiology, reproduction and demography (see Christian & Weavers, 1994; Phillips, 1995; James, 1996). In this study, we conducted research by way of radio-telemetry to understand three aspects of the spatial ecology of immature Komodo dragons:

(1) Describing movement patterns of hatchlings following emergence from their nest as a basis to gain an insight into the initial natal dispersal tendencies in this species.

(2) Estimating differences in the movement capacity and activity areas (i.e. a subset of home ranges used during a defined time period; see Thompson *et al.*, 1999) of hatchling and juvenile Komodo dragons.

(3) Determining basic patterns of habitat use in hatchling and juvenile Komodo dragons.

These three facets of study are considered to be important in acquiring fundamental ecological information about this species and are likely to contribute considerably to improving its management by increasing an understanding of its habitat requirements. For Komodo dragons, which occupy a limited geographical range and whose populations are fragmented across islands, knowledge of hatchling and juvenile dispersal could potentially be important in influencing metapopulation dynamics. Similarly, habitat requirements throughout ontogeny are essential to understanding those resources (e.g. food or habitat), which, if disturbed by humans, could perturb population processes of Komodo dragons, a priority conservation species in Indonesia.

Materials and methods

Study site

The study was conducted in the Loh Liang valley (9.4 km^2) on Komodo Island, (8°33′40″S and 119°29′51″E) in Komodo National Park (KNP) (Fig. 1), East Nusa Tenggara, Indonesia. Vegetation cover of KNP has been described elsewhere (e.g. Auffenberg, 1981). Komodo Island is a rugged, mountainous island covered predominantly by savannah grassland. Deciduous monsoon forests dominated by Tamarind tree *Tamarindus indica* are found in coastal valleys, while closed evergreen forest persists on hills above 500 m altitude. The mean daily field temperatures (sourced from a data logger located at sea level in Loh Liang valley) during the period of this study averaged 29.5 ± 0.1 °C and varied within 1.5 °C between months and 0.2 °C between years.

Study animals

Five hatchling Komodo dragons with a mean SVL of 20.16 ± 0.85 cm (SEM) (range 18.25–22.6 cm) and a body mass of 0.11 ± 0.01 kg (range 0.095–0.135 kg) were captured following emergence from their nest. Hatchlings were captured by hand or in PVC pipe traps (10 cm diameter and 100 cm in length) on emergence from their nests. Seven juvenile Komodo dragons (mean and SEM of SVL 55.81 $\pm$ 2.97 cm and body mass of 3.03 ± 0.56, range 1.4–5.7 kg) were captured by hand or in baited box traps. We could not determine the sex (i.e. a potential covariate underpinning differences in spatial ecology) of these 12 individuals, as this requires the use of genetic sexing techniques (Halverson & Spelman, 2002), which currently have not been tested on our sample set (C. Ciofi, unpubl. data).

Radio-telemetry techniques

This study was conducted between March and June over 2 years (2004–2005). In 2004, two hatchlings and four juveniles were radio-tracked, and in 2005 three hatchlings and four juveniles were followed. Telemetry equipment consisted of activity-sensitive AVM G31 V transmitters (AVM Instruments Co. Ltd., Colfax, CA, USA), an AVM LA12Q receiver and a three-element Yagi antenna. Transmitters were attached to the dragon's tail using duct tape.
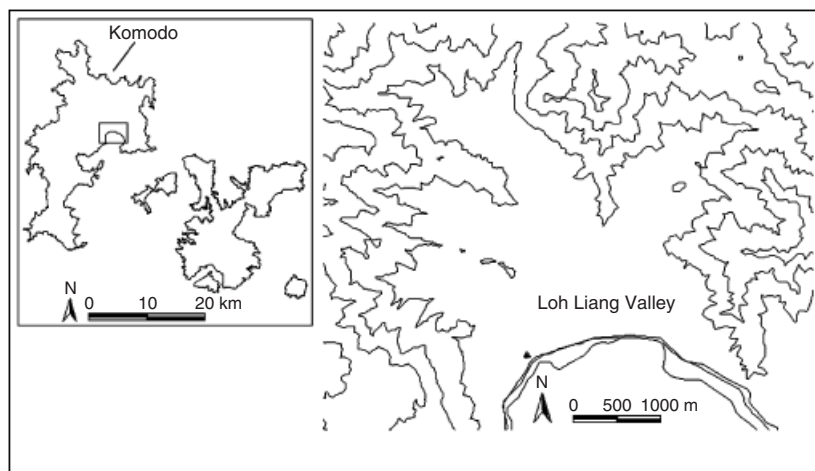
Figure 1 Location of the study site in the Loh Liang valley on Komodo Island, the largest island in Komodo National Park (inset). Contours are at intervals of 100 m.

After the transmitters were attached, hatchlings and juveniles were released immediately. Each animal was radio-tracked for 7–56 days (mean 31.42 ± 5.05 days). Initial observations showed that radio-tracked Komodo dragons never moved during the night. To increase independence of the data, individual daily observations were made in four sessions, separated by a minimum daily time interval of 2–3 h. Daily positions and habitat-use observations were made from 06:00 to 18:00 h across four time periods of 06:00–09:00, 09:00–12:00, 12:00–15:00 and 15:00–18:00 h.

Fixes were collected by either direct observation or by triangulation (Samuel & Fuller, 1996; Fitzgerald *et al.*, 2002; Ciofi *et al.*, 2007). Fixes were recorded using a Global Positioning System (GPS; Garmin Etrex, Olathe, KS, USA), and then recorded into an excel spreadsheet and visualized onto digital topographic maps using ArcView 3.1 (Environmental System Research Institute, Redlands, CA, USA).

Habitat use

To quantify, and compare, the habitat use of juvenile and hatchling lizards, we collected data on habitat and shelter site parameters concurrently with their positions obtained during radio-tracking (Olupot & Waser, 2001). Four parameters were measured and defined as follows:

(1) Habitat strata defined as the use of either terrestrial or arboreal strata.

(2) Habitat type defined as the presence of lizards in one of three key habitat types including open deciduous forest, closed dense forest and savannah grassland. These habitat types were readily distinguished by canopy closure and floristic composition.

(3) Shelter site included a description of resting or sleeping location based on the use of vegetation (identified to species) or substrate type. Further, with relation to vegetation, particularly trees, tree diameter at breast height (Dbh) and tree height were also recorded. Tree height and the Komodo dragons' height above ground were calculated using a Suunto clinometer PM5 (Suunto, Finland).

(4) Elevation the elevation at which a lizard was located was recorded alongside every positional fix.

Habitat selection

To identify broad-scale patterns of habitat selection in Komodo dragons, we scored both the vegetation type (closed forest, open forest and savannah grassland) and elevation occupied by the dragon at each position as a measure of habitat selection. These observed habitat characteristics were then compared with a dataset of similar measures drawn from 209 randomly generated locations (each scored for habitat type and elevation) within the study valley. We selected the number of random points based on the average number of habitat fixes collected from both hatchling and juvenile Komodo dragons to ensure a balanced design for statistical purposes. Comparisons between the observed and random habitat positions were used as a basis to determine whether dragons utilized habitat in a non-random manner.

Data analysis

Movement and orientation

Patterns of path movement (linearity) of Komodo dragons were estimated using directionality and tortuosity analysis (Nams & Bourgeois, 2004). Directionality was analyzed by measuring the turning angle of movement on each point in a compass direction (Claussen, Finkler & Smith, 1997). The turning angles indicate the movement angles between two consecutive points (Higham, Davenport & Jayne, 2001). Tortuosity was measured by analyzing the fractal dimension (D), whose values range between 1 and 2; at $D = 1$, the animal's path of movement is straight. In contrast, when $D = 2$ (i.e. maximum), the animal's path of movement is so tortuous as to cover a plane completely (Nams & Bourgeois, 2004). To describe site fidelity, we ran the Site Fidelity Test (with 1000 replications) to obtain the r^2 value; the lower the r^2 value, the higher the site fidelity of an animal. Directionality and site fidelity were computed using the Movement Program extension (Hooge, Eichenlaub & Solomon, 1999) and X Tools of ArcVIew 3.1 (ESRI), while fractal dimensions were computed using the computer program Fractal (Nams, 2004).

Komodo dragon movement distances were calculated as the distance moved between two consecutive points (Samuel & Fuller, 1996). The mean daily movement distance was obtained by dividing the total distance of recorded movements by the total number of radio-tracking days (Phillips, 1995; Fitzgerald *et al.*, 2002; Ibrahim, 2002). These calculations were made using the Animal Movement Program (Hooge *et al.*, 1999) and X Tools extension of ArcView 3.1 (ESRI).

Activity area

Activity areas were calculated using two methods: the 100% minimum convex polygon (MCP) and the adaptive kernell analysis (AKA) representing 95 and 50% of the probability distribution of animal locations (Samuel & Fuller, 1996). The 95% AKA is believed to be a very effective method for estimating the internal structure of activity areas, and provides one of the least biased estimates of home range size (Samuel & Fuller, 1996). The 50% AKA has been widely used to determine the core area or habitat use in other reptiles (Kernohan *et al.*, 1998; Fitzgerald *et al.*, 2002). In this study, the estimate from the 50% AKA method was used to determine core areas within the activity area of hatchling and juvenile Komodo dragons. Activity area estimations were calculated using the Animal Movement Program (Hooge *et al.*, 1999) in ArcView 3.1 (ESRI). Individuals with < 10 fixes (i.e. hatchling 64CDC09 and juvenile 6EDB3B7) were not included in this analysis.

Statistical analysis

Pre-analysis, all continuous data were log transformed to meet assumptions of parametric statistical tests (Zar, 1999). Log-transformed data failing these assumptions were analyzed using non-parametric statistical procedures. Categorical data were analyzed using χ^2 statistical procedures.

Results

Patterns of movement

During our study, hatchlings moved in a predominantly linear fashion with little movement over previously occupied areas (Fig. 2, animals a and b). In contrast, juvenile dragons exhibited much more tortuous movement paths, reflecting increased activity over the same area (Fig. 2 animals c and d). Fractal analysis indicated that the movement paths undertaken by hatchlings $D = 1.11 \pm 0.009$ were significantly more linearly directed (i.e. strait) than that of juvenile dragons ($D = 1.39 \pm 0.05$; Mann–Whitney U test; $Z = -2.56$, $P = 0.011$). Moreover, the degree of site fidelity in hatchling ($r^2 = 729\,502.68$) was significantly less than that of juveniles ($r^2 = 2\,729\,220.96$; t-test; $t_{1,9} = -39.12$, $P \leq 0.001$).

Hatchlings were significantly less active than juvenile dragons and, on average, moved $32.62 \pm 12.67\,\mathrm{m\,day}^{-1}$ compared with $129.14 \pm 41.71\,\mathrm{m\,day}^{-1}$ (t-test; $t_{1,9} = -3.014$, $P = 0.015$). Furthermore, the longest daily movements recorded by hatchlings ($163.99 \pm 22.96\,\mathrm{m\,day}^{-1}$) were significantly less than those of juvenile dragons ($509.87 \pm 73.32\,\mathrm{m\,day}^{-1}$) ($t$-test; $t_{1,9} = -5.24$, $P = 0.001$). The daily activity of hatchlings was significantly less than juvenile dragons (χ^2test; $\chi^2 = 51.68$, $P \leq 0.001$) based on the relative proportion of movement fixes compared with the proportion of stationary fixes.

Activity area size

The activity areas of hatchling and juveniles ranged between 1.72–4.83 ha and 4.03–61.77 ha for MCP, 12.14–20.12 ha and 5.49–33.23 for 95% AKA and 2.51–4.74 and 0.56–10.48 ha for 50% AKA, respectively (see Table 1 and Fig. 3). Hatchlings used significantly smaller activity areas: approximately eight times less than juveniles for the 100% MCP (t-test; $t_{1,9} = -3.658$, $P = 0.006$). However, there were no significant differences in 95% AKA (t-test; $t_{1,9} = -0.018$, $P = 0.177$) and neither for 50% AKA (t-test; $t_{1,9} = 0.396$, $P = 0.702$). In five of six cases, the activity areas of juvenile dragons overlapped with one ($n = 4$) or two ($n = 1$) conspecifics and the extent of this overlap ranged from 4.84 to 91.00% or from 2.55 to 6.65 ha.

Habitat preferences

Hatchling and juvenile Komodo dragons significantly differed in the parameters of habitat use. Hatchlings were predominantly arboreal (97.7% arboreal vs. 2.30% terrestrial), while juveniles were predominantly terrestrial (28.96% arboreal vs. 71.04% terrestrial) (χ^2 test; $\chi^2 = 239.22$, $P \leq 0.001$; Fig. 4a). On average, hatchlings remained on the same tree for 9.5 days (SEM = ± 3.17) before moving to the next tree. Hatchlings were rarely observed on the ground, except during long-distance movements between trees ($>30\,\mathrm{m}$). We observed an occasional arboreal movement whereby hatchlings were able to move between trees with overlapping canopy. Juveniles, on the other hand, spent significantly less time on trees (average of 3.17 days SEM = ± 0.75) (t-test; $t_{1,8} = 2.257$, $P = 0.038$). Body size was a better indicator of habitat use, as there was a highly significant negative linear relationship between body size and amount of arboreal habitat use (%arboreal
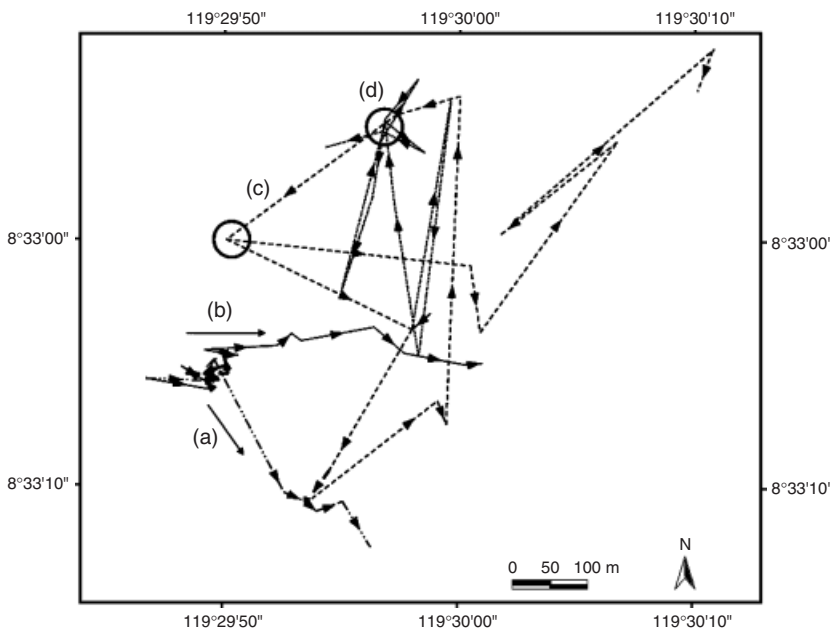
Figure 2 Examples of the movement pattern of hatchling (a and b) and juvenile (c and d) Komodo dragons *Varanus komodoensis*. The arrows indicate the direction of movements, and circles represent nocturnal shelter sites.

Table 1 Summary of results on the movements and activity areas of hatchling and juvenile Komodo dragons *Varanus komodoensis*

Animal ID (PIT tag)	SVL	Total movement (m)	Mean daily movement (m)	Longest daily movement (m)	Activity area 100% MCP (ha)	Activity area 95% AK (ha)	Activity area 50% AK (ha)	Tracking duration (days)	Number of fixes
Hatchlings									
64E4218	22.6	983.39	70.24	191.19	4.82	20.12	4.73	14	50
63DFB2A	18.25	571.60	15.04	195.08	1.71	13.06	3.60	38	66
64D4C0E	18.30	692.91	23.09	96.62	1.95	13.47	2.51	30	51
63C1383	20.35	949.37	22.07	173.08	3.58	12.14	2.70	43	67
Mean	20.16 ± 0.85	799.32 ± 99.82	32.61 ± 12.67	163.99 ± 22.96	3.02 ± 0.73	14.70 ± 1.83	3.39 ± 0.51	31.25 ± 6.34	58.50 ± 4.63
Juveniles									
64CF2AO	61.85	2286.24	326.60	397.86	12.53	33.23	10.477	7	18
639E332	68.35	6308.95	143.38	791.58	32.37	16.34	2.327	44	39
643761C	58.05	350.71	43.84	334.34	4.02	5.49	0.558	8	18
64E2E95	55.45	2879.15	89.97	427.53	17.41	32.55	2.451	32	14
63DE6F1	51.15	5556.63	99.22	672.06	61.77	30.51	4.301	56	57
63D9C4B	44.45	3445.53	71.78	435.83	17.75	21.56	2.650	48	44
Mean	55.81 ± 2.97	3471.20 ± 892.46	129.13 ± 41.71	509.87 ± 73.32	24.31 ± 8.38	23.28 ± 4.49	3.79 ± 1.42	32.5 ± 8.52	31.67 ± 7.15

SVL, snout–vent length; MCP, minimum convex polygon; AK, adaptive kernell.

activity $= -2.070 \times SVL + 139.244$, $r = 0.965$; ANOVA, $F_{1,9} = 108.423$, $P = 0.001$; Fig. 4b).

Both hatchling (χ^2 test; $\chi^2 = 45.86$, $P \leq 0.001$) and juvenile Komodo dragons (χ^2 test; $\chi^2 = 85.04$, $P \leq 0.001$) were observed most frequently in open deciduous forest, compared with either closed dense forest or savannah. There was no significant difference in the frequency of observed habitat preference use between hatchlings and juveniles (χ^2 test; $\chi^2 = 1.89$, $P = 0.389$; Fig. 4c). However, immature Komodo dragons were observed to occupy habitat types significantly different from a randomly assigned distribution of habitat locations (χ^2 test; $\chi^2 = 25.45$, $P \leq 0.001$; Fig. 4c). Relative to the occupancy distribution of random locations among habitat types, Komodo dragons were observed more prevalently to occupy open deciduous forest and less likely to occupy either closed forest or savannah habitats.

With respect to elevation, there was a significant preference for hatchlings to be located in the lowest elevation class (54.55% < 25 m above sea level) (χ^2 test; $\chi^2 = 20.98$, $P \leq 0.001$). Juvenile dragons (χ^2 test; $\chi^2 = 9.26$, $P = 0.002$) exhibited a significant preference for elevations between 25 and 50 m (36.17%) above sea level. Elevation use for hatchlings and juvenile dragons was significantly different (χ^2 test; $\chi^2 = 25.127$, $P = 0.0001$). Furthermore, elevation preferences between hatchlings (χ^2 test; $\chi^2 = 53.707$, $P \leq 0.001$) and juveniles (χ^2 test; $\chi^2 = 29.736$, $P \leq 0.001$) differed significantly from a random selection of elevations within their environment.

Shelter sites

Shelter sites were defined as those places used by hatchlings and juveniles for resting (also as sites between movements – for juveniles only) or as overnight refuges. Hatchlings used trees exclusively for shelter. They significantly used live (84.71%) over dead trees (15.29%) (χ^2 test; $\chi^2 = 122.859$, $P \leq 0.0001$). Among live trees (15 spp. recorded), there was

a significant tendency for hatchlings to occupy Tamarind trees *Tamarindus indica* (45.37%) (χ^2 test; $\chi^2 = 122.859$, $P \leq 0.001$). Juveniles used predominantly crevices under or among rocks ($51.77 \pm 5.72\%$) as shelters. These shelters were found in forested area with significant granitic exfoliation (i.e. rocky fields). Juvenile Komodo dragons, albeit infrequent, used nine tree species for resting or basking.

Discussion

Distinct ontogenetic differences in movement, activity area and habitat use were evident between hatchling and juvenile Komodo dragons in the Loh Liang valley on Komodo Island. In particular, movements of hatchling dragons were largely linear compared with those of juveniles that occupied a defined activity area (i.e. a component of their home range). The rate and distance moved by hatchlings within their natal valley was up to 75% less than juveniles. Limited spatial overlap (i.e. tortuosity) of movement and the reduced rates of daily movements would explain the much-reduced activity areas estimated for hatchlings compared with juveniles. Combined, these attributes of the post-natal spatial ecology of hatchling *V. komodoensis* are evidence for dispersal resulting in hatchlings moving as far as possible away from their nests relative to the actual distance travelled. Over the month-long period of radio-tracking, hatchlings had moved up to 500 m from their nests. Other studies in lizards have detected differences in natal dispersal tendencies, with some species being relatively sedentary (i.e. remain in close proximity to natal hatching/birth sites) (Olsson & Shine, 2003; Sumner, 2006) to others being more irruptive and moving away from their hatching/birth sites (Doughty & Sinervo, 1994). Two major hypotheses are suggested to explain the differences in natal dispersal tendencies including avoidance of inbreeding and a reduction in resource competition among conspecifics (Olsson & Shine, 2003). From our results, given the relatively small time
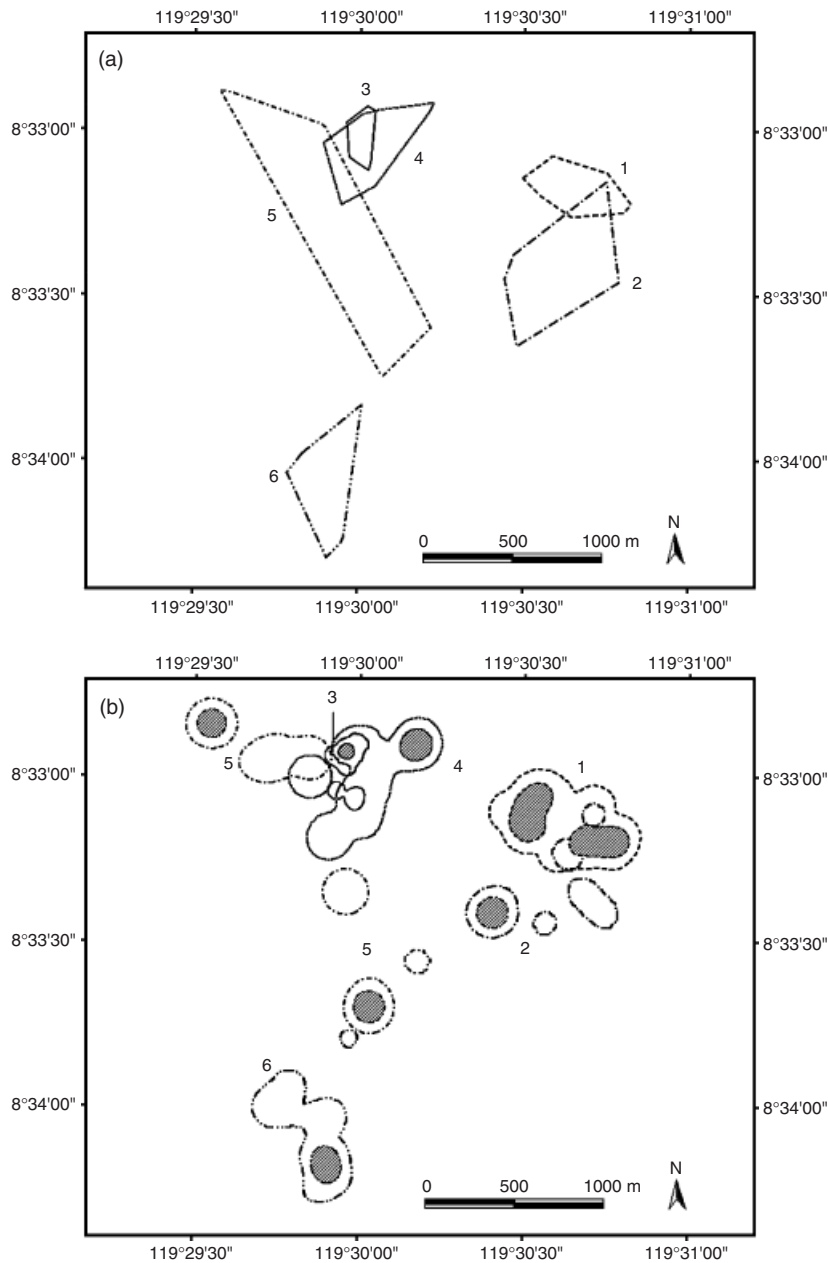
Figure 3 Activity area overlap of six juvenile Komodo dragons *Varanus komodoensis* as calculated by minimum convex polygon (a) and adaptive kernell (50% hatched areas & 95% outer line) (b). Numbers refer to juvenile ID as follows: (1) 64CF2A0, (2) 639E332, (3) 64E761C, (4) 64E2E95, (5) 63DE6F1, (6) 63D9C4B.

frame (1–2 months) used to follow the animals, we were unable to determine the termination of natal dispersal (i.e. the point at which a hatchling begins to use a defined home range) and thus cannot comment on what may be the predominant selection pressure associated with these movements.

The highly arboreal nature of hatchling Komodo dragons compared with the much more terrestrial-based activity of juveniles is a clear indication of an ontogenetic habitat shift between these two immature life phases. Arboreal habitat use by hatchling Komodo dragons is considered to be of a response to some of the selection pressures that trigger ontogenetic habitat shifts observed in other lizards and snakes (Stamps, 1983; Irschick, 2002; Keren-Rotem, Bouskila &

Geffen, 2006). In particular avoidance of larger conspecifics, well known for intraspecfic predation (Auffenberg, 1981), would seem an intuitive reason for Komodo dragon hatchlings to remain predominantly arboreal. Similarly, prey availability which is likely to be determined by the relatively small jaw gape of hatchlings could predispose arboreal activity to obtain suitable sized prey such as geckoes (observed in this study), skinks and large insects (Auffenberg, 1981). Other than predation and food availability, intraspecific competition, thermoregulation, morphological constraints and shelter sites are additional hypotheses that could necessitate arboreal activity in hatchling Komodo dragons (Stamps, 1983; Huey, 1991; Keren-Rotem *et al.*, 2006). Experimental manipulation
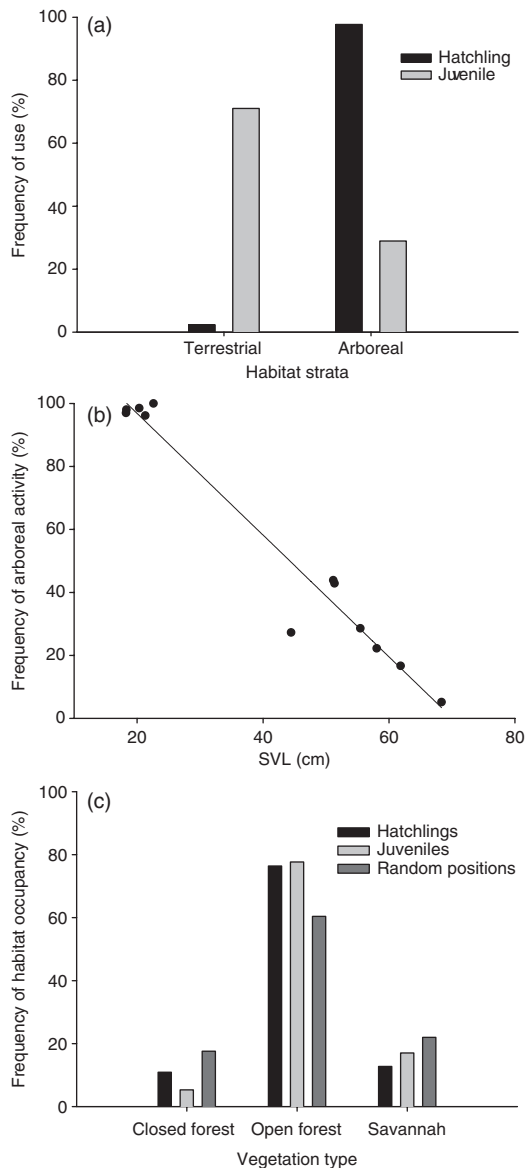
Figure 4 Differences between hatchling and juvenile Komodo dragons *Varanus komodoensis* with respect to terrestrial versus arboreal habitat use (a), the relationship between their body size and arboreal activity (b) and differences in habitat use (c).

of these factors, although logistically difficult, could quantify the relative importance of specific mechanisms to explaining arboreality in hatchling Komodo dragons.

The ontogenetic transition to a more terrestrial based activity appeared largely size dependent (Fig. 4b) and thus individual Komodo dragons underwent a gradual shift towards terrestrial activity rather than any discreet transition. Presumably, with increased body size, relaxation of some selection pressures that necessitate arboreality (e.g. conspecific avoidance) and the increasing need to acquire larger terrestrial prey could underpin habitat use transitions

in juvenile Komodo dragons. As terrestrial activity increased juvenile dragons occupied discreet areas of habitat underpinning an activity area (i.e. a subset of their home-range). The size of juvenile activity areas was estimated (using MCP) at 24.31 ± 8.38 ha, an area 800% larger than hatchlings but only 5% of the activity area estimated for adult Komodo dragons (Ciofi *et al.*, 2007). Size related differences in an individuals space use are well recognized in reptiles and often linked with increased utilization of resources (Christian & Waldschmidt, 1984; Perry & Garland, 2002; Pearson, Shine & Williams, 2005). In most instances there were some degrees of overlap in the estimated activity areas of juvenile Komodo dragons. However, within their activity areas, the 50% kernell analysis identified smaller more frequently used areas that were exclusively occupied by a single individual. While we have not tracked all individuals that could overlap with our focal animals, on closer examination of their core movement areas, there was often the presence of an individual's overnight shelter area. In an ontogenetic context, core areas, while frequently used at particular points in time, are subject to change with age/ size or even seasonally, again depending on resource availability (e.g. King & Green, 1999). The individual's sex appears to be another important covariate underpinning spatial ecology in adult reptiles (Perry & Garland, 2002). In this study, however, sex could not be determined from either external examination or on probing the cloaca for the presence of hemipenes. Thus, we are unable to ascertain whether sex was a significant covariate linked to spatial use in immature Komodo dragons.

With respect to patterns of broad-scale habitat use, both hatchlings and juveniles were found to significantly utilize open deciduous forest compared with either closed forest or the more xeric savannah grassland. Among these different habitat types, it is suspected that immature Komodo dragons could encounter highly different regimes of prey, shelter, predators, competition, parasites and temperature (Dunham, Grant & Overall, 1989; Huey, 1991). These differences are likely to strongly influence an individual's fitness (Huey, 1991). For example, aversion of savannah grassland by immature Komodo dragons could be envisaged due to low densities of small prey but also that the thermal environment is uniformly hot with little shade, which might limit the capacity of small dragons to thermoregulate effectively. In contrast, the open deciduous forest provides a mosaic of thermal conditions, higher prey productivity and shelter, which are likely to be important habitat elements influencing habitat use in small Komodo dragons. The low-frequency use of closed forest by immature dragons is suspected of being negatively biased due to the relatively low proportion of its availability (17.6%) relative to the other two predominant habitat types (60.4 and 22.0% for open forest and savannah, respectively).

Conclusions

Radio-tracking of immature life stages of the Komodo dragon revealed several key features of their spatial ecology.

On emergence, hatchling Komodo dragons became arboreal and moved in a largely linear fashion away from their nest. The lack of overlap in their movements suggests that this early life stage is associated with a period of natal dispersal. At this stage, we have very limited direct evidence for how far hatchlings might disperse. For example, from the hundreds of marked hatchlings we have released to date as part of a long-term population ecology study, only a single individual has been recaptured and in this case the juvenile had remained within its natal valley one year after its birth. However, indirect information from population genetics has indicated significant sub-structuring among valley populations, perhaps indicating that there may be limited dispersal across all size classes over evolutionary time frames (Ciofi & Bruford, 1999). With respect to the management and conservation of this species, given the strong reliance of immature animals on open deciduous forest for food and shelter, clearing of this habitat for agriculture or timber would represent a major threat that would severely impact the survival of immature Komodo dragons. At present, within KNP, enforcement of habitat protection appears to be adequate to prevent major changes in habitat structure.

Acknowledgements

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