Territorial and site fidelity behavior of *Lyriocephalus scutatus* (Agamidae: Draconinae) in Sri Lanka

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Abstract.—This study on territorial behavior of *Lyriocephalus scutatus* suggests that territorial behavior is an important component of the life history of the species. *Lyriocephalus scutatus* belongs to the monotypic genus *Lyriocephalus*, and apparently its uniqueness, placing it in its own genus, extends to its strange behavior and atypical site fidelity. To understand this territorial behavior, two populations were observed while continuously recording other factors influencing territorial and site fidelity behaviors. Individual lizards performed various behaviors in their daily active periods on tree trunks and on the ground. They also exhibited highly specific synchronized territorial behavior among other individuals in the same population. Behavioral patterns differed between males and females, and the degree of "aerial horizontal distribution" of *L. scutatus* seems to be a novel behavior among lizards. Individual *L. scutatus* are highly territorial over other individuals of the same sex, as adult males observed in the study sites solely performed their territorial displays on a specific tree, whereas females occupied the largest territories.

Key words. Territorial behavior, Lyriocephalus scutatus, Lyre head lizard, Sri Lanka

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Introduction

Sri Lanka is a continental island endowed with high herpetofaunal diversity and endemism. Two-hundred and seven species of reptiles have been described from Sri Lanka and more than half are endemic to the island (Somaweera and Somaweera 2009). The agamid lizard fauna of Sri Lanka is comprised of 18 species in six genera, 15 of which are endemic (Bahir and Surasinghe 2005; Samarawickrama et al. 2006): Calotus (six species; four endemic), Ceratophora (five species; all endemic), Cophotis (two species; both endemic), Lyrocephalus (one endemic species), Otocryptis (two species; both endemic), and Sitana (one species of unclear taxonomic status). Of these genera, Lyrocephalus, Ceratophora, and Cophotis are are considered to be relict lineages because they are confined to Sri Lanka.

In spite of the uniqueness of the lizard fauna of Sri Lanka, little is known with regard to the behavior, ecology, and natural history for most of the agamid species. This is particularly true with regard to territoriality, even though males of most species are presumed to be territorial. Among the short observation notes on territorial behavior of Sri Lankan agamids are works by Deraniyagala (1931, 1953), Smith (1935), Bambaradeniya et al. (1997), and Karunarathna and Amarasinghe (2008). However, there have been no long-term studies on ter-

ritorial behavior of any Sri Lankan agamid lizard. One species, *Lyrocephalus scutatus*, is of particular interest because it is the only species of the genus and is endemic to Sri Lanka (Figs. 1 and 2). Several authors, (Deraniyagala 1931, 1953; de Silva et al. 2005; Manamendra-Arachchi 1998) reported *L. scutatus* to have territorial behaviors with males intimidating each other by opening wide their blood-red mouths showing their long sharp teeth and shaking their heads. Additionally, when threatened, they would lie motionless on their sides feigning death. A better understanding of these behaviors is necessary to more completely appreciate the unique lizard fauna of Sri Lanka and to aid in its conservation. Hence, the present study examines territorial and site-fidelity behavior of the endemic lizard *L. scutatus*.

Methods and materials

Study area

The study took place in the Gannoruwa Forest Reserve [GFR] (7° 17' N, 80° 36' E) in Kandy district in the Central Province of Sri Lanka (Fig. 3; modified from Wickramasinghe 2006). The reserve is a remnant forest patch covering an area of ~250 acres and is surrounded by villages. The vegetation within the GFR can be grouped into

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natural forest, naturalized plantations (i.e., abandoned cocoa, tea, coffee, *Artocarpus heterophyllus*, etc.), grasslands, and mahogany plantations. Home gardens comprise most of the anthropogenic ecosystems bordering the reserve. Observations were made at two sites within the GFR. Site A at Pallegama (07° 28' N and 80° 60' E) is a high canopy home garden that is very well shaded by the common tree *Myristica fragrance* (Fig. 4) with a moderate to steep slope (30° average). Site B at Yatihalagala (07° 36' N and 80° 52' E) is also a shady habitat, but with greater human interference than study Site A since it is nearer to human settlements (Fig. 5). Garmin (GPS12) was used to obtain geographical coordinates and Brunton clinometers (Brunton Company, USA) were used for measuring slope.

Methods

Detailed studies started in mid October, 2005, and were conducted until late February, 2006. Both field sites were partitioned into a grid of 1×1 m quadrats using small PVC stumps to mark the coordinates so locations of lizards could be determined within 0.25 m. Two template grid maps were created, one for each of the study sites. Each lizard observed was captured, sexed, measured, and given an identifying name. To permit identification of individual lizards from several meters away, all individuals observed and captured, within the study areas, were temporarily marked using loose elastic bands of various colors placed on the waist. Three reproductive classes were recorded: adult males, adult females, and subadults. Adult males and females were defined as individuals that were sexually mature (i.e., >80 mm snout to vent length [SVL] and with fully grown rostral knob and crest). Subadults were defined as individuals that were not in breeding condition (i.e., <80 mm SVL and less developed rostral knob and crest). Direct visual observation of natural populations was aided, when necessary, by the use of a pair of Nikon 10 × 8 binoculars. Focal population sampling was conducted by observing the entire population continuously for 20 to 60 minutes; thus the observed focal time for individual animals of a particular population was equal. If a particular animal was not located during the entire sampling it was considered "Not Observed."

In order to gather detailed information on spatial distribution, censuses were conducted three times a month by traversing the entire field site. Trees in which lizards were observed were scanned throughout the day (0600 to 1800 hr) and the locations of all lizards (marked or unmarked) were recorded. All behaviors observed, including both those exhibited in isolation and those directed towards other individuals, were recorded and all individuals involved in social interactions were noted. A total of 110 hours was spent performing the censuses.

Herein, an individual lizard's territory is considered to be the area that encompasses all positions of the lizard, day and night. Thus, all locations where individuals were observed during the study period (including incidentally observed individuals) were recorded and mapped for the calculation of the size of the territory. Territories are graphically displayed as polygons with inside angles ≤180° hand-drawn around the outermost observed coordinates. In addition, all woody surfaces of trees where lizards were recorded were added to the area of the territory using average cylindrical area representing the trunk of a tree (Philibosian 1975). Since we have repeated measurements of the same individuals on different days, and multiple individuals from the same site (spatial autocorrelation) data were analyzed statistically as a linear mixed effects model using software R-2.9.0win32. Microsoft Office Excel 2007 was used for the graphical display of data.

Results

Observed behaviors

A total of 180 focal animal samples were recorded from 12 marked individuals (six males, three females, and three subadult males) on 15 days (including night visits) over a six-month period in the pre-reproductive season of these lizards. The marked population at Site A consisted of five individuals (two males, one female, and two subadults). The marked population Site B consisted of seven individuals (four males, two females, and one subadult). All behaviors demonstrated, including both those exhibited in isolation and those directed towards other individuals, are summarized in Table 1.

Table 1. Summary of commonly observed behaviors of lizards in their natural environment.

Behaviors	Description		
Body-lift	Uplift on all four limbs pushing body off surface followed immediately by descent, repeated frequently; other lizards may or may not be seen in the vicinity.		
Gular Sac Display	Gular sac is extended with lateral side compression accompanying a Body-lift.		
Head-bob	Relatively rapid up-and-down movement of the head or head and neck region only; gular sac may also be extended.		
Tail-wag	Undulating movement of tail.		
Still	Positioned on the surface without notable movements.		
Adjustment	A simple change in still position.		
Walking	Moving about in an area slowly.		
Feeding	Taking in a food item.		



Natural forest
Grassland
Mahogany plantation

Figure 3. Map of Gannoruwa Forest Reserve - Kandy district Sri Lanka.

Figure 1. Lyrocephalus scutatus – male.



Figure 2. A lizard threat pose – *Body-lift, Gular Sac Display*, and *Head-bob*.



Figure 4. Study site A - Gannoruwa Pallegama.

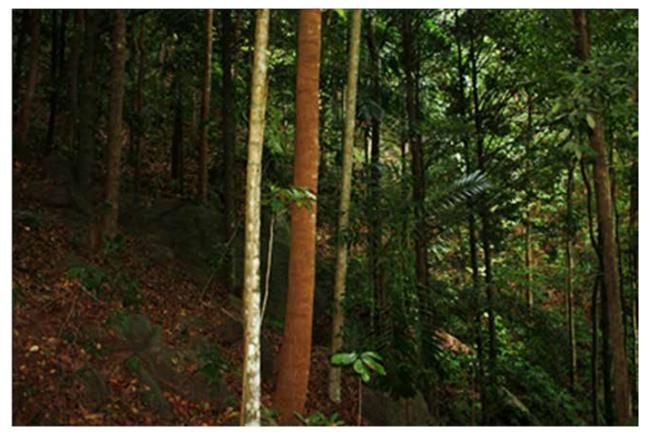


Figure 5. Study site B - Gannoruwa Yatihalagala.



Figure 6. Different behaviors observed: Body-lift, Gular sac display, and Head-bob with Body-lift.



Figure 7. Different behaviors observed: Tail wag, Adjustment, and Still.

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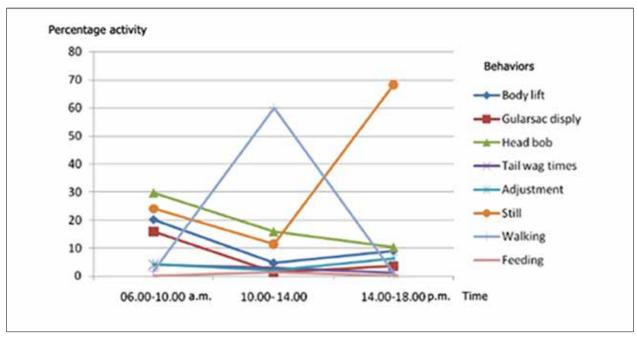


Figure 8. Percentage of various behaviors displayed by L. scutatus according to time of day.

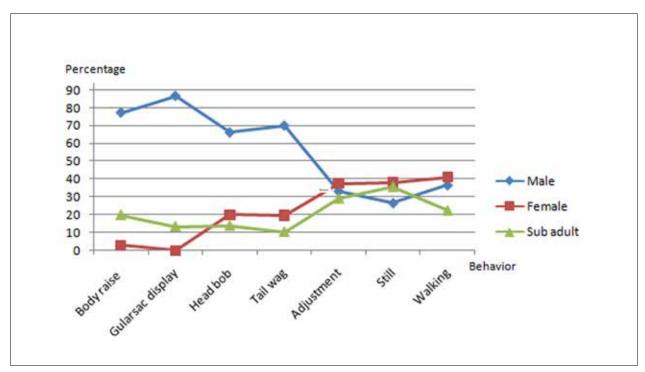


Figure 9. Percentage of time spent exhibiting various behaviors for the different reproductive groups of *L. scutatus*: males, females, and subadults.

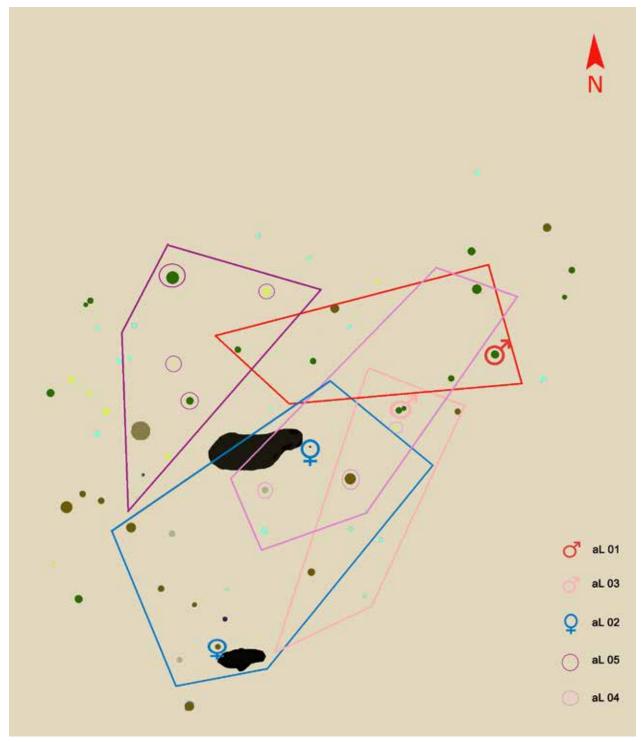


Figure 10. Map of individual territories of lizards in site A.

Table 2. Percentage of overlap of territories between individuals according to reproductive category.

Category	Male	Female	Subadult
Male	<1.0%	40%	20%
Female	48%	00%	11%
Subadult	15%	18%	00%

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Several different behaviors were observed during lizard activity periods (Figs. 6 and 7). Generally, displaying would begin in the morning and continue for several hours until the displaying lizards would climb down from trees to the ground. In the evening, lizards would climbup the trees and start displaying again until they would go to sleep at nightfall. When an individual lizard did not comedown from the tree, it remained there in the *Still* position the entire day. When lizards were displaying they performed their behaviors in an upright position on the tree trunks. *Body-lift*, *Gular Sac Display*, *Head-bob*, and *Tail-wag* were frequently performed in the upright position, however *Head-bob*, *Body-lift*, and *Tail-wag* were also performed on the ground while performing *Walking* or *Feeding*.

The meeting of two different individuals was not observed during the six-month study period. On one occa-

sion, a female was found with a male on the same tree, but no remarkable behaviors were observed between those two individuals, although the male did display its usual behaviors.

Behavioral differences among reproductive groups

Time spent performing the various behaviors differed with the time of the day (Fig. 8). Behaviors such as *Head-bob*, *Body-lift*, *Gular Sac Display*, and *Still* were common in the morning hours from 0600 to 1000 hr. *Feeding* was not observed during this morning time period and only a small amount of time was spent *Walking*. *Tail-wag* and *Adjustment* were also performed in the morning. During daytime, from 1000 to 1400 hr, *Walking* increased to about 60% of the behavior of *L. scutatus*. All the other behaviors observed in higher proportion during

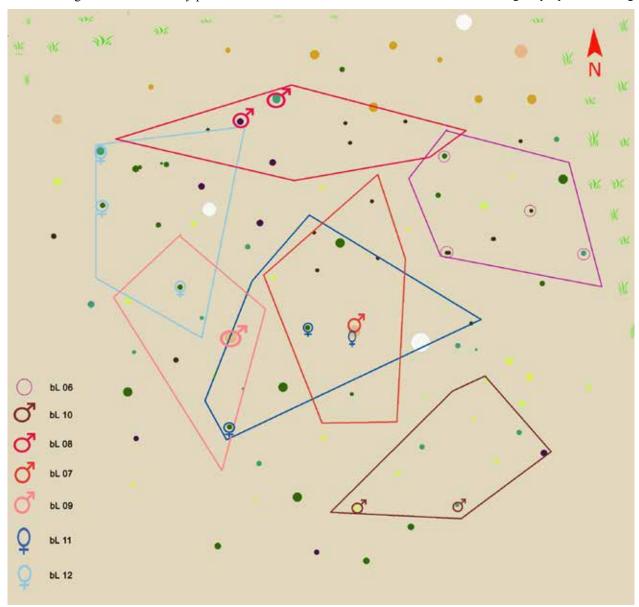


Figure 11. Map of individual territories of lizards in site B.

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the day gradually decreased in frequency as time passed. Evidently 90% of *Feeding* was done in the midday hours (1100-1230 hr). During the evening hours from 1400 to 1800 hr, *Still* was demonstrated by 70% of the individuals observed, and all the other behaviors became rarer, especially *Walking* and *Feeding*.

Overall, the behaviors exhibited by the lizards varied with time from morning to evening. Additionally, all individuals at a particular site would synchronize their behavior. For example, when a certain individual would begin the *Gular Sac Display*, all individuals at that particular site would soon perform the *Gular Sac Display*

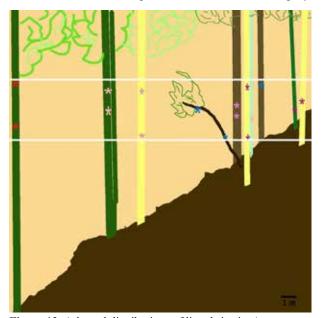


Figure 12. Arboreal distributions of lizards in site A.

as well. Normally the dominant male would initiate the display with other individuals following with the same A paired t-test showed that there is a significant difference in the patterns of behaviors between males and females (t = 3.10, p = 0.004). Not only were the behaviors shown by males and females markedly different, the percentages of time spent in each behavior differed as well (Fig. 9). Body-lift and Gular Sac Display were confined to males and Head-bob and Tail-wag were shared by both sexes, but males had a comparatively higher percentage. About 60% of the observed instances of Adjustment, Still, and Walking were performed by females.

One instance of mating behavior of *L. scutatus* was observed in this study. The single observation was about 2.4 m above the ground at 0720 hrs in the morning on a *Syzygium aromaticum* tree with a girth of 42 cm. Copulation was maintained for three minutes, after which both individuals were observed in the same tree for the duration of the day.

Territoriality

The size of territory differed among reproductive groups with females having the largest $(264.94 \pm 59.8 \text{ m}^2)$, followed by males $(178.72 \pm 32.1 \text{ m}^2)$, and then subadults $(174.73 \pm 32.3 \text{ m}^2)$, although males and subadults had roughly equal sized territories (Figs. 10 and 11). A Paired t-test showed a significant difference between male and female territories (t = 2.38, p = 0.02). Territory size was not linked to the body size of the owner (t = 2.8, p = 0.008).

On five occasions male territories were overlapped by approximately 40% by a female territory and on four



Figure 13. Arboreal distributions of lizards in site B.

occasions male territories were overlapped by approximately 20% by a subadult territory (Table 2). Only on one occasion did a male territory overlap another male territory, although this overlap involved less than 1.0% of each territory. On six occasions female territories were overlapped by approximately 48% by a male territory, and on a single occasion a female territory was overlapped by approximately 11% by the territory of a subadult. On three occasions, subadult territories were overlapped by approximately 15% by a male territory and on a single occasion a subadult territory was overlapped by approximately 18% by the territory of a female. Overlap of territories among the same reproductive group was not observed in this study except on the single occasion of the two males with territories overlapping less than 1.0%. In fact, all males observed in the two study sites were on a tree with no other lizards present (marked with male symbol in Figs. 10 and 11), and they remained on "their" tree throughout the study period with the single exception of the lizard "bL 08" which was recorded occupying two different trees. Males displayed only when they were on their particular tree. Females and subadults were recorded on several trees within their particular home range.

Arboreal distribution

As a group, the lizards of this study showed a previously unreported behavior of maintaining a particular level of height on the trees, especially while displaying. When the observed lizards climbed-up trees they all appear to stop at a similar and consistent elevation. In Site B all the individuals maintained an arboreal height of 2.5 m to 4.1 m, and since the area is rather flat their distribution approximately paralleled the ground. It was only at these positions in the trees that the lizards performed synchronized display behaviors (Figs. 12 and 13). In Site A, which has a slope of 30°, the level of the height of lizards forms about a 60° angle to the ground. Interestingly, at Site A, when the dominant male started to adjust its position all other lizards at the site adjusted their positions, thus maintaining the same height. Individuals in Site B imitated the same pattern of horizontal arboreal plane display among the group.

Discussion

The marking technique we employed proved successful. The use of bands to mark lizards permitted identification of individuals from several meters away and throughout the entire study period because the bands remained in place the entire time. The bands did not reflect sunlight and did not dislodge with shedding of the skin. Furthermore, the presence of the bands did not appear to increase predation vulnerability since the bands were thin and somewhat covered by the hind limbs. This method



Figure 14. Ceratophora tennentii in Tangappuwa, Dumbara (Knuckles World heritage), Sri Lanka.

can be used as a temporary, noninvasive marking technique for other behavioral studies of lizards, instead of the traditionally-used toe clipping, which injures lizards and can alter their behavior.

Lyriocephalus scutatus showed clear territorial maintenance and site fidelity behaviors at the two study sites at Gannoruwa Forest Reserve. The territorial behavior of *L. scutatus* is a daily-synchronized behavior, initiating with a morning display session followed by ground *Walking*, and in the evening another display session. Behaviors included in territorial maintenance and site fidelity include *Body-lift*, *Gular Sac Display*, *Head-bob*, and *Tail-wag*.

Observations and time budget analysis of the behaviors of the studied lizards show that *Body-lift*, *Head-bob*, Gular Sac Display (shown only by males), and Tail-wag are important for site fidelity behavior. When lizards display there is a regular order of behaviors (Jennings and Thompson 1999) that begin with Body-lift followed by Head-bob. While doing Head-bob the Gular Sac Display is also performed. Tail-wag is rare, but when performed it is normally after these previously mentioned behaviors. While lizards are displaying they always hold their Body-lift for a long time and while performing other behaviors simultaneously. Observed male lizards held their Body-lift from five to 30 minutes, and it is suspected that this might help them appear larger and help in mate attraction. Gular Sac Display is only exhibited by males and may be important in sexual selection (Stuart-Fox and Ord 2004). Body adjustments help lizards to locate one another. The upright position of display in *L. scutatus*, combined with their laterally placed movable eyes on the top of their head, enables them to see others in the group in such a way that lizards are able to distinguish other individuals by their side view.

Many anurans exhibit synchronized calls known as "chorus" behavior (Narins 1992). Likewise, *Lyriocephalus scutatus* shows synchronized territorial maintenance behaviors within a particular group (i.e., individuals within the group display their territorial behaviors simultaneously). When one particular individual starts to display, the other individuals in the same group eventually start their display as well. Synchronized territorial maintenance behavior is important for the recognition of the territory of a particular individual relative to all other individuals in the group from one point of view.

In general, among agamid lizards of Sri Lanka males are known to be territorial (Deraniyagala 1931, 1953; Manamendra-Arachchi 1998; de Silva et al. 2005) and they show territorial behaviors more than females and juveniles. Therefore, it is not entirely surprising that males of *L. scutatus* show *Body-lift*, *Gular Sac Display*, *Headbob*, and *Tail-wag* whereas females do not. *Adjustment* and *Still* are not territorial maintenance behaviors because all three reproductive groups show them in nearly equal frequencies, with males showing a slightly lower frequency than the others.

Subadults showed the highest frequency of *Walking* among the observed behaviors. This may be due to the process of acquiring a permanent territory. Males were generally more active than females. This disparity between the sexes suggests that *Body-lift*, *Gular Sac Display*, *Head-bob*, and *Tail-wag* are vital territorial maintenance behaviors since they occur most frequently in males.

The three genera Lyriocephalus, Ceratophora, and Gonocephalus are consistently placed within the same clade of the acrodont lizard phylogeny (Macey et al. 2000). Ceratophora (Sri Lankan horned lizards) and Lyriocephalus are sister taxa (Schulte et al. 2002), while Gonocephalus, is the closest Southeast Asian relative of Lyriocephalus (Macey et al. 2000). The territorial behavior of the endemic Leaf-nosed horned lizard (Ceratophora tennentii) is somewhat similar to L. scutatus as observed in previous fieldwork (Fig. 14). They perform Body-lift and Head-bob but there is a clear difference in the way they hold the body in Body-lift; Ceratophora tennentii holds its body with a curvature of the spinal column while positioning the legs in similar manner to that of L. scutatus. Observations on Gonocephalus sp. (Fig. 15) in Lambir Hills National Park, Sarawak, Malaysia show a similar territorial behavior to that of *L. scutatus*, with Body-lift and Gular Sac Display being performed in a similar manner.

The results presented here show a large difference in the size of male and female territories. Females have



Figure 15. *Gonocephalus* sp. in Lambir Hills National Park, Sarawak, Malaysia.

larger home ranges compared to that of males, which may be due to highly territorial nature of males, and females mainly moving about for feeding and mating. The female territories always overlapped with that of males, which suggests that a single male has access to one or two females. Subadults, on the other hand, have territories that overlap with females and adult males. This may be due to them not being of breeding size and thus not a threat to the resident adult males.

Territory size was not linked to the body size of the owner. The size of the territory might depend on the slope and other physical factors of the land, vegetation cover of the study area, structure of the forest, or human interference in the area. Males had their own defended tree and they do morning and evening displays while perched on that tree. On one occasion a female was found on one of the trees occupied by a male.

This study shows that adult males of *L. scutatus* are highly territorial. Individual males maintain their territories, although their territories can overlap with females and male subadults. Adults of arboreal *Anolis* spp. usually occupy vertical territories such as trees and walls. Since a lizard defends all of the area in which it is found, except perhaps resting and egg laying sites, territory is almost equivalent with home range (Philibosian 1975; Jennings and Thompson 1999). Generally, a lizard spends the entire daylight period moving from one frequented perch site to another, often spending several minutes at a single site. A typical perch position is with the body vertical and head pointing toward the ground at

various angles. The primary activities within the territory include feeding, copulation, and defense, the latter usually against members of the same species and sex, and of similar size. Adults tend to stay in one territory until death, while younger animals are more mobile. Juveniles are usually spatially separated from adults, perching on small rocks and low vegetation. Subadults are often tolerated within adult territories and territories of males and females may overlap (Jennings and Thompson 1999).

Conclusion

The arboreal distribution of the individuals of L. scutatus in the same group is a significant behavior and may be novel. This behavior seems to permit the individuals within a group to spot all or most of the other individuals at once, thus increasing the communication among individuals within the group. Further study should be performed to investigate this peculiar behavior of L. scutatus more thoroughly. Within the short period of time allowed for the present study, the arboreal distribution of individuals in same group is the foremost finding and it gives us evidence of the hidden eccentric behaviors that agamid lizards possess. Moreover, it may be that other territorial agamid lizards show a similar aerial horizontal distribution and synchronizing display as well. What is clear is that future studies on the behavior of agamid lizards of Sri Lanka are needed since much of their ecology remains unknown.

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