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Dimensions of Home Range Structure of *Agama agama* in the Savanna Region of Nigeria

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Abstract.—**Home Range (HR) evaluations provide data related to animal searches for food, mates, and other resources. In grasslands of Nigeria where populations of the semi-arboreal African Rainbow Lizard (*Agama agama*) are dense, I measured three dimensions of HR: home range area (HRA), home range length (HRL), and vertical height (VH). I surveyed 3–4 h in each of four sites between 0600–1300 and 1600–1800 over 6 d each month (June 2015 to May 2016). I recorded sighting grid coordinates and vertical positions of the lizards. After correction to 95% resolution, I programed the coordinates to calculate HRL (and VH) by Adjusted HRL method, and calculated HRA by Minimum Convex Polygon (MCP) method. Highest daily mean HRA (618 m^2), HRL (63 m), and VH (262 cm) were for mature males during the dry season. Mature females, juvenile males, and juvenile females, in decreasing order, had lower means for all three dimensions of HR. Age, sex and age-sex classes, as well as seasonal changes had significant influences on mean values of HRA, HRL, and VH. Regression analysis indicated that HRL is a significant predictor of HRA. There were age-sex class frequency overlays in all HR dimensions. I recommend a multi-dimensional approach to HR investigations for *A. agama* (and other semi-arboreal lizards) because of its possible link to age-sex class resource partitioning among other habitat-use interactions.**

Key Words.—commensal; grassland; movement; reptile; tropical; West Africa

Introduction

The African Rainbow Lizard (*Agama agama*) inhabits many types of open habitats across much of Africa, including cleared forest lands (Yeboah 1982; Pauwels 2004; Oleg et al. 2012; Akani et al. 2013). This lizard has also made inroads into the hitherto uncolonized island of Madagascar (Wagner et al. 2009) and is establishing populations in southern Florida (Wilson and Porras 1983; Bartlett and Bartlett 1999; Enge et al. 2004). Male *A. agama* are conspicuous in color, especially during breeding season, with variation across its geographic range (Enge et al. 2004; Wagner et al. 2009; Mediannikov et al. 2012). The breeding season in northern Nigeria coincides with the rainy season (late May to October). The head of adult males is orange or purple-indigo, the torso is deep blue to near black, and the tail is bluish-black at its distal end, a description also noted by Harris (1964) and Madsen and Loman (1987). Adult females are dull grey with dorsal yellow to orange markings.

Agama lizards in Nigeria appear to be partly commensal with humans (Sura 1987), benefiting from human-created habitat in townships and villages without being targeted for extermination, as are some rodents because of Lassa fever concerns (pers. obs.). An active predator, *Agama* pursues several kinds of invertebrates as well as small vertebrates, though they may also adopt a sit-and-wait strategy (Gupta 1982). Depending on locality and prey availability, *A. agama* behaves opportunistically, feeding mainly on insects but sometimes eating fruits and berries and seeds and flowers (Chapman and Chapman 1964; Gupta 1982; Pauwels 2004; Vasconcelos et al. 2014; Rabiu 2019). It also eats the young of its own species, small birds, small snakes (Cloudsley-Thompson 1981), and chick hatchlings (pers. obs.). *Agama agama* is also a predator of smaller lizards on the Santo Antão Island of the Cape Verde archipelago (Vasconcelos et al. 2014).

An important parameter for understanding the biology of most vertebrates is the home range (HR) of an individual, and Burt (1943) defined HR as that area traversed by an animal during foraging, mating, and other routine activities. In general, HR is an indicator of resource requirements of an animal in relation to their availability in the environment. Factors known to affect HR sizes in vertebrates are season, weather, age, sex, and activity pattern (Stickel 1968; Mysterud et al. 2001). In the Savanna region of Nigeria, rainfall is seasonal. The timing of its onset, amount and duration of the season directly influence the abundance of insect prey for the lizards, hence indirectly affecting their HR sizes. Madsen and Loman (1987) studied *A. agama* in Kenya and reported that mature males had larger home range sizes than females, but not larger than that of subordinate males.

I describe the HR structure of *A. agama* in terms of its area and the linear distances moved by lizards (home range length) in the Savanna region of Nigeria. I determined age and sex class differences and the effect of season on HR structure of the lizard. *Agama*

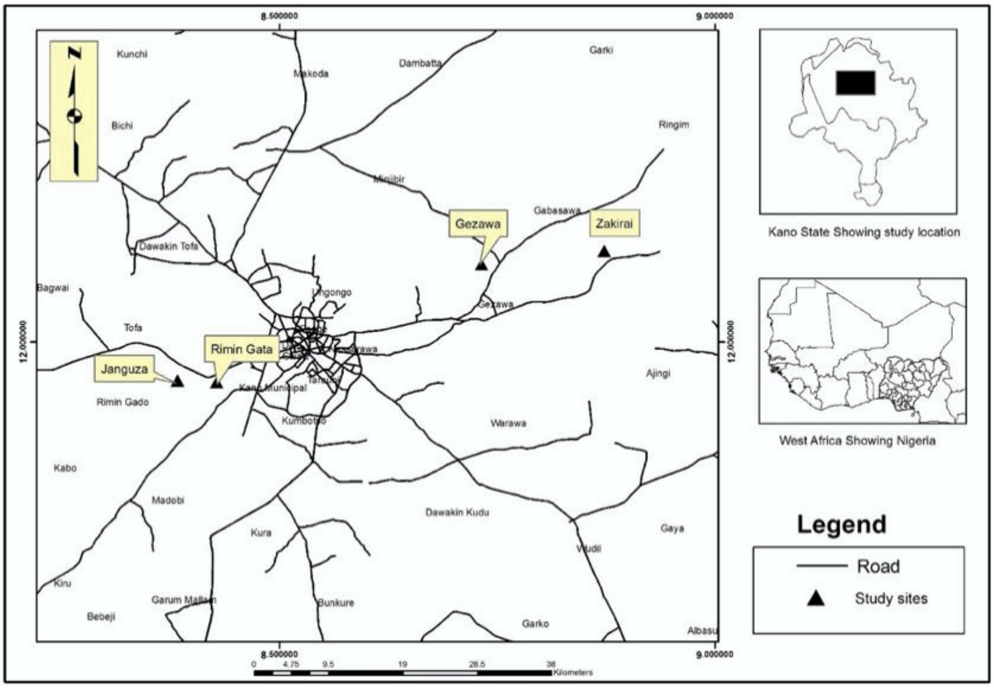

Figure 1. Site locations of study outside Kano, in the north of Nigeria. Insets are Kano provincial and the West Africa regional maps.

agama is semi-arboreal (Spawls et al. 2002; Enge et al 2004; Chirio and LeBreton 2007; Mediannikov et al. 2012) and individuals may perch against a steep surface throughout the night, spending several hours during the day basking, foraging, and even mating while still perched on these surfaces (pers. obs.). Because the concept of HR is directly concerned with movements related to these vital activities of foraging, mating, and other efforts, I also considered this vertical component of its movement.

Materials and Methods

***Study area*.—**I studied *A. agama* within the Savanna vegetation belt of northern Nigeria, in the vicinity of the Kano area (Fig. 1). Two of four study sites, Jan Guza, 2.05 ha (11°59′35"N, 8°19′49"E; 480 m elevation) and Rijiar Zaki, 3.20 ha (11°58′59"N; 8°23′18"E; 467 m elevation) were to the west of Kano city. To the east were two other sites near the townships of Gezawa, 2.95 ha (12°05′26"N; 08°45′48"E; 448 m elevation) and Zakirai, 3.05 ha (12°05′27"N; 08°53′13"E; 411 m elevation). In these areas, rains are seasonal from late May to early October, the period when *A. agama* breeds, and the dry season lasts from late October to mid-May (Fig. 2). The rainy season commenced approximately three weeks prior to the first sampling date in June 2015. I terminated work in May 2016, early in the next rainy season.

Because the climate and landscape in the grassbelt of northern Nigeria are rather uniform, all four sites had several common species of plants and animals; however, the Jan Guza and Rijiar Zaki sites tended to be moister and had relatively more vegetation cover than the sites at Gezawa and Zakirai. The latter two sites had more human presence and partially constructed buildings. While most natural forbs and grasses have been replaced by agricultural weeds, there are still some remnants of indigenous tree species, which, in order of abundance included Tamarind (*Tamarindus indica*), African Locust Bean (*Parkia biglobosa*), Silk Plant (*Albizia echvalieri)*, African Plum (*Parinari macrophylla*), Giant-leaved Fig (*Ficus lutea*), Marula (*Sclerocarya birrea*), and White Thorn (*Acacia albida*). In addition to native plants, there were also some exotic trees and shrubs amid abandoned construction sites. Human activities near

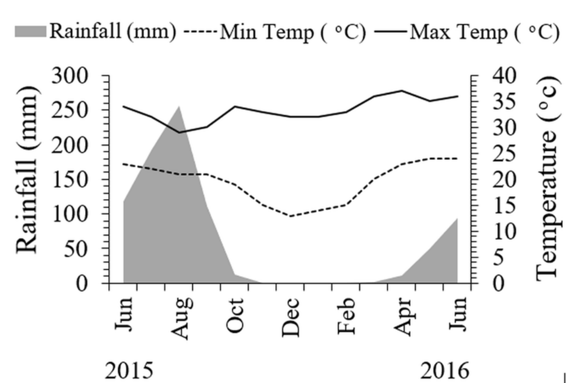

Figure 2. Precipitation and temperature records from the general study area south of Kano, Nigeria during the period of study, June 2015 to May 2016.

the study sites included seasonal rain-fed farming, with crops that included Guinea Corn (*Sorghum bicolor*), Peanuts (*Arachis hypogea*), and occasional Watermelon (*Citrullus lanatus*). The main arthropod taxa, which represents the primary food base for *A. agama* across all sites, included Diptera, Hymenoptera, Isoptera, and Orthoptera (Rabiu 2019).

Movement surveillance.—I divided each of the four study sites, with surface areas ranging from 2.5–3.05 ha, into 5 × 5 m grids, similar to those in Rose (1982), and I marked grids with numbered flags tied to thin rods pegged into the ground. I marked vertical locations of sightings by scratching or chalk-painting the spot, and then held a graduated ranging pole upright at 90° to the ground surface and aligned it to the marked spot to determine its height above ground. I completed 3–4 h survey walks, mostly from 0600–1100 and 1600–1800, for at least 6 d per month to determine home range area (HRA), home range length (HRL), and vertical height (VH) of lizards. I used visual surveys with occasional use of binoculars to determine the location of lizards. I was able to clearly distinguish numerous lizards from each site through the combination of their apparent size, depth of tone, body bruises, damaged tail, and other physical attributes. For any lizard that lacked distinguishing features, I caught them by hand or intercepted and guided them into a large meshed jute bag. I uniquely painted lizards using concentrated aqueous leaf extract of Henna, *Lawsonia inermis* (150 g dried leaf powder/40 ml distilled water brewed overnight). The Henna leaf extract is safe and widely used on the human body (Zumrutdal and Ozaslan 2012) and is considered an appropriate marking method for lizards (Beausoleil et al. 2004). I tracked the same lizards sighted in subsequent months whenever possible, but when they disappeared or were lost, I tracked another lizard of the same age-sex class. I considered home range parameters separately for these lizards.

Estimates of HRA, HRL, and VH.—Following the Adjusted Range Length method described by Stickel (1954), I added a half distance between flags (= 2.5 m) to each end of the distance between the most widely separated sighting locations. I collected all observations in all sites opportunistically. To enhance the stability of individual home range with increased sightings, I considered only lizards with 65 or more sightings for the analysis (58 records being the threshold for stable home range values). After correction to 95% resolution, I programmed grid sighting records into MATLAB (Version R2013b 2016) for the calculations of HRA using the Minimum Convex Polygon (MCP) method (Southwood 1966; Haenel et al. 2003), and both HRL and VH as a linear measure. Then I computed the mean values of HRA, HRL, and VH for each age class (adult and juvenile); sex (male and female), and age-sex (adult male, adult female, juvenile male, and juvenile female) classes, as well as the statistical range. I used Analysis of Variance (General Linear Model because of differing sample sizes) to compare age, sex, age-sex, and seasonal differences. I also tested the association between HRA and HRL by Regression to determine if it was possible to predict HRA from HRL. All analyses were completed using Minitab statistical software, Version 18.1 2017 and I set the level of statistical significance at $P \leq 0.05$.

Results

Home range area.—The mean HRA of all lizards was 510.4 m^2 (Table 1). Male *A. agama* had HRA sizes that exceeded 700 m^2, with two having up to 800 m^2. Only one adult female had HRA of greater than 600 m^2. Mean male HRA was significantly greater than that of females ($F_{1,221}$ = 214.02, P < 0.001). There also was a significantly higher mean HRA for all adults (539.2 m^2) compared to 429.6 m^2 for juveniles (429.6 m^2; $F_{1,221}$ = 14.16, P < 0.001; Table 1). There was a pattern of decreasing mean HRA sizes in the order: adult males, adult females, juvenile males and juvenile females (Table 1). The differences of HRA indicate a significant age-sex class influence on HRA sizes ($F_{1,221}$ = 84.12, P < 0.001).

The effect of seasonal change on HRA was evident from larger home range sizes during the dry season than in rainy season (Table 1). The difference, as with the influence of age and sex classes, was also significant ($F_{1,221}$ = 40.58, P < 0.001). A fixed-effect test showed the months with the highest precipitation (July, August, and September) as the period contributing most to the significant seasonal difference, by reduced HRA sizes ($F_{11,213}$ = 4.60, P < 0.001). There were no significant differences in HRA between any of two sites or among the four sites ($F_{3,221}$ = 2.22, P = 0.086). The HRA size frequency overlay among age-sex groups were common when individual HRA sizes were between 350 and 680 m^2 (Fig. 3).

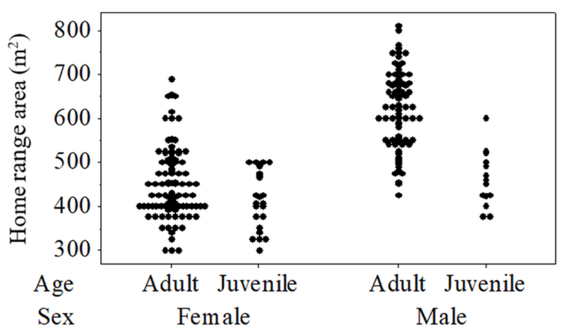

Figure 3. Individual plot frequencies of home range area (m^2) for lizards with 65 sightings and 95% resolution by age-sex classes aggregated for samples from four study sites of the African Rainbow Lizard (*Agama agama*) in Nigeria.

Table 1. Means, standard errors (in parentheses), and ranges of values (below mean) for home range area, HRA (m^2), home range length, HRL (m) and vertical height, VH (cm) for various lizard classes and seasons in African Rainbow Lizard (*Agama agama*) from June 2015 to May 2016, in the grassland of northern Nigeria. The dataset represents 65 sighting records per lizard with 95% resolution for sighting points.

Category	Class	n	HRA	HRL	VH
Lizards	All lizards	225	510.4 (7.8) 300–810	53.8 (1.08) 25.0–105.4	193.9 (8.6) 0–492
Age-Sex	Adult Males	86	618.8 (9.46) 300–690	61.8 (1.8) 27.5–105.4	262.3 (15.4) 0–489
	Adult Females	101	449.1 (7.95) 425–810	51.7 (1.2) 25.0–74.5	171.8 (9.9) 0–446
	Juvenile Males	14	428.5 (16.9) 375–600	43.6 (4.0) 25.0–72.5	112.4 (29.2) 0–328
	Juvenile Females	24	412.3 (13.1) 300–500	39.4 (2.1) 25.3–60.5	89.7 (11.6) 0–191
Age	Adults	188	539.2 (8.6) 300–810	57.4 (1.1) 25.0–105.4	217.2 (9.4) 0–492
	Juveniles	37	429.5 (11.2) 300–600	40.6 (2.0) 25.0–72.5	109.0 (13.2) 0–447
Sex	Males	100	591.3 (7.0) 375–810	57.3 (1.8) 25.0–105.4	205.8 (14.8) 0–492
	Females	125	440.4 (10.1) 300–690	48.1 (1.1) 25.0–74.5	120.4 (8.8) 0–328
Season	Dry	87	547.5 (13.6) 300–800	59.7 (1.4) 41.2–105.4	203.1 (14.7) 0–481
	Rain	138	484.2 (8.3) 300–810	45.7 (1.2) 25.0–101.1	188.1 (10.6) 0–492

Home range length.—The mean home range length, HRL, for all lizards sampled was 53.8 m, a value that is only lower than those for all adult lizards (male and female), adult males, and the mean dry season HRL (Table 1). Sex class difference in HRL between males and females (Table 1) was significant ($F_{1,221} = 25.77$, $P < 0.001$). Similarly, age class difference indicated that adult lizards had moved significantly longer distances (longer HRL) than juveniles ($F_{1,221} = 14.10$, $P < 0.001$). With age-sex classes of the lizards, there was decreasing mean HRL in the following order: adult males, adult female, juvenile males, and juvenile females, which were significantly different ($F_{3,221} = 18.90$, $P < 0.001$). There was a seasonal effect on HRL with significantly longer distances moved during the dry season than in the rainy season ($F_{1,221} = 54.91$, $P < 0.001$).

Vertical height movement.—By age class, the mean vertical height, VH, moved by adult *A. agama* was twice that of juveniles (Table 1) and the difference was significant ($F_{1,221} = 23.16$, $P < 0.001$). The mean VH for males was significantly higher than of females ($F_{1,211} = 27.42$, $P < 0.001$). The ranking of the classes in order of decreasing height was, adult males, adult females, juvenile males, and juvenile females (Table 1) and the differences were significant ($F_{3,221} = 19.94$, $P < 0.001$). Seasonal difference between the dry and rainy seasons had no influence on vertical height movement by *A. agama* ($F_{1,223} = 0.710$, $P = 0.400$).

Relationships among HRA, HRL, and VH.—The 3-dimensional relationship among HRA, HRL, and VH of *A. agama* movements appears to show two clusters of HRs (Fig. 4). Adult females and juveniles of both sexes are in one cluster, and adult males are in the other cluster, with noticeably greater values for all three dimensions of HR than those of the other three age-sex classes (Fig. 4). HRL was a significant predictor of HRA ($t = 9.27$, df $= 2$, $P < 0.001$, $r^2 = 0.36$), with the equation of best fit as HRA = 297.6 + 3.96 HRL.

Discussion

Effect of age, sex and age-sex classes on HR structure.—Because there are few HR studies that focus specifically on *A. agama* (Leaché 2005), comparisons to the present study must be drawn from lizards of related taxa, or other lizards in general. The HR values I estimated for male *A. agama* follow a common pattern with other agamids for which the male HR sizes appeared to be significantly larger than those for females (e.g., Madsen and Loman 1987; Znari and Benfaida 2001; Perry and Garland 2002), and in numerous other lizard taxa (e.g., Wone and Beauchamp 2003). Sex class

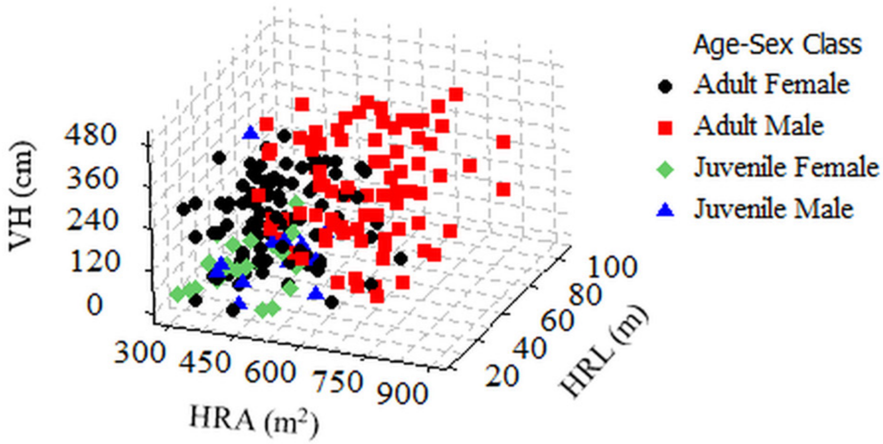

Figure 4. The 3-dimensional movement structure by age-sex classes in the African Rainbow Lizard (*Agama agama*) in Nigeria. All values were from 95% resolutions of sighting records. Abbreviations are HRA = home range area, HRL = home range length, and VH = vertical height.

differences in HRA for *A. agama* might simply be related to differences in body size, with males able to traverse larger areas than females by virtue of being bigger, which is directly related to their energetic requirements (Perry and Garland 2002). There are data for several lizard species, however, that show that even with HR corrected for body size, mean male HR was larger than that of females (Perry and Garland 2002), which could mean that there are sex influences on HR apart from size differences of lizards.

The mean HR of *A. agama* in Kenya was 556 m^2 (Madsen and Loman 1987), which compares favorably with the mean of 591.3 m^2 that I found. In this study, the authors recorded marked sex class difference, which they attributed to male polygamous tendencies that would lead to males trying to include many females into their territories. The mean HR size for females from the Kenyan study, however, was 197.0 m^2, which was much smaller than mean 440.5 m^2 that I found. The localities sampled by Madsen and Loman (1987), especially along the Tana River banks, Kenya, appeared to be richer (in terms of moisture, vegetation, and presumably invertebrate prey) than the habitats I sampled in northern Nigeria, except, perhaps during the rainy season. Given the association between food abundance and home range size (Rose 1982), possibly higher resource availability in the Kenyan sites might explain why *Agama* HR sizes were relatively smaller than what I found in northern Nigeria. Similarly, a study of Bibron's agama (*A. impalearis*) in Morocco reported a mean HR of 3,600 m^2 (Znari and Benfaida 2001), a 700% higher value than the overall mean of 510 m^2 that I found. The larger HRA for *A. impalearis* could have been due to the arid, food-poor conditions in Morocco, which might cause lizards to search a larger area for food in a habitat that sharply contrasts with the seasonal, rain-fed, grassland of northern Nigeria, a region relatively richer in terms of insect and seeds.

Agama agama, however, is also a slightly larger lizard than *A. impalearis*, which should have had larger or equivalent sized HR to *A. impalearis*, but I did not find this. Thus, there might be some influence of habitat type (and perhaps, dietary resources) on HR sizes. I did not specifically test the influence of body size on HR; I simply grouped the lizards into adults and juvenile classes, and not by individual body mass *per se*. Nonetheless, I did find significant effect of age class such that mature, larger lizards showed larger HR sizes than juveniles. Overall, HR sizes of *A. agama* that I found appear to be influenced by age, sex, and age-sex classes, and given significant seasonal HR size difference, most probably also by dietary supplies.

Seasonal differences in HRA and HRL.—I found seasonal differences in HR, with greater area and longer lengths of HR during the dry the season, despite the inhibiting effects of lower temperatures and cold conditions on lizard activity during the tropical winter of northern Nigeria. This may be related to food differences. Food supplies (insects, other invertebrates, and plant materials) are poorer in the dry season (November to April) than in the core rainy season period of June through to October (Rabiu 2019). Breeding in *A. agama* during the rainy season coincides with the availability of high-quality insect (i.e., non-ant) and seed foods (Rabiu 2019). The availability of prey items within short distances during the peak rainy months and shortly after (i.e., July to early October) had probably decreased the need for wider and extended movement, resulting in significantly lower HRA and HRL sizes. Experiments that supplemented food to Side-blotched Lizards (*Uta stansburiana*), a non-agamid species, resulted in slower habitat use and slower growth of home range size than unfed lizards (Waldschmidt 1983), implying that food scarcity might induce rapid expansion of home range.

Vertical dimension of HR.—Male *A. agama* occupied higher vertical positions than females and juveniles. The topmost status of vertical height (VH) for the adult male lizards appears to be similar to that found for *A. impalearis* in Morocco (Znari and Benfaida 2001) and for Black-necked Agamas (*Acanthocercus a. atricollis*) in northern South Africa (Reaney and Whiting 2003). The higher VH values for *Agama* males, and their general tendency to keep high vantage vertical height range, especially in the dry, non-breeding season (November-April) also appeared to be related to certain uses, such as to hunt for orthopterans and coleopterans. Prey are probably more readily viewed and attacked from higher vertical positions than lower levels (Rabiu 2019) and could be indicative of behavioral dominance of males (Harris 1964). Noticeably mature males may keep almost entirely above ground at levels higher than 2 m, while females and juveniles of both sexes remain near or at the ground level. This space partitioning may remain that way for several days, without any mature female or juvenile of either sex reaching the vertical height of the adult males. Adult females and juveniles ascended to higher vertical positions only when adult males were absent. I found that one male during 3 d of a sampling period never left a perch.

Despite the importance of vertical habitat in this species, I am not aware of any prior study of the home range of *A. agama* that included this parameter. Fully arboreal species have received more attention. For example, Reaney and Whiting (2003) found no age or sex influence on the type of tree selected by the arboreal *A. a. atricollis* in South Africa, although trees with larger diameter were generally preferred. There may be methodological difficulties in the measurement of HR sizes for arboreal and saxicolous species, which consistently have lower HR sizes than those of terrestrial species (Perry and Garland 2002). The VH should have important consideration in the analysis of the movement structure in *A. agama*, as well as that of other semi-arboreal species, because of its probable link to age-sex class hunting strategy or resource partitioning (Rabiu 2019) and possibly other habitat-use and behavioral interactions.

Predictability of HRA from HRL.—I found a significant relationship between HRA and HRL that would allow the prediction of HRA sizes using HRL values. Hence, for the purpose of monitoring the populations of *A. agama*, decision could be made to collect only the HRL data, which can be accomplished more easily. Because VH is not always a feature in the movement repertoire of *A. agama* in certain treeless or flat terrains, only the relationship for the HRA and HRL may be desirable for use to describe the relationship between a predictor and response variables, as well as help predict new HRA observations. Where baseline data is required and is unavailable, however, I recommend that all three dimensions of HR structure, HRA, HRL, and VH be collected.

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