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Spatial and Behavioural Segregation Between *Agama agama* and *Agama weidholzi* Living in Sympatry in Southern Senegal

MASTER'S THESIS

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Declaration

I hereby declare that I have done this thesis entitled “Spatial and behavioural segregation between *Agama agama* and *Agama weidholzi* living in sympatry in Southern Senegal” independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 20th March 2020

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Michal Semrád

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Abstract

This Master´s thesis is focused on evaluation of sympatry between *Agama agama* and *Agama weidholzi* living in Southern Senegal and its aim is to find out similarities and differences of habitat use and behaviour between the observed species. The site of the observation is Toubakouta town that is situated in Southern Senegal in unique nature habitat of Delta river Saloum where both species coexist in sympatry. They live in urban areas side by side which was not previously reported. Daily field monitoring data collection was divided into tracks and performed by sight or binocular. The collected field data were recorded on a paper sheet and GPS coordinates were registered by Geo tracker. Analyses of processed data were performed in Excel 2007, ArcGIS 10.1, and Statistics (version 25.0). We observed 325 individuals in total, 154 were *Agama agama* and 171 *Agama weidholzi*. The results indicate that *Agama agama* can be found in both man-made and natural habitat while *Agama weidholzi* almost exclusively inhabits man-made habitat. In man-made habitat, *A. agama* prefers to occupy the tops of walls and roofed walls more frequently compared to *A. weidholzi*. *A. agama* does not choose habitat according to the presence of vegetation. If vegetation is present, the height of basal vegetation is lower than in *A. weidholzi*. The escape direction is mostly upwards. *A. weidholzi* tends to populate places with the presence of vegetation. The height of basal vegetation is higher than in *A. agama*. The escape direction is mostly downwards, but there are also significant incidences of escapes upwards and to other side of the wall. Up until now, *Agama weidholzi* has not been well studied and further research is needed.

Key words: Common Agama, House Agama, Rainbow Lizard, Gambia Agama, Reptiles of Senegal, Toubakouta, Coexistence of Agama Lizards

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IUCN – International Union for Conservation of Nature

CPA – Categorical Principal Components Analysis

1. Introduction and Literature Review

1.1. Introduction

The habitats of the savannah and tropical forest in West Africa are highly diverse. For this reason, the West African region is characterized by a high degree of biodiversity and endemicity (Krishnan et al. 2019).

The focus of our study is on Agama lizards. In Africa, the agamas are the most widespread and abundant reptiles (Leaché 2009). They are also the most diverse group of Squamata on the African continent (Leaché et al. 2014). Thanks to several certain attributes, such as relatively larger size, strict diurnality, high activity, high population density and social grouping in many species, agama lizards have become an excellent object for exploring of several biological researches focused on ecology, behaviour, evolution, adaptive radiation, etc (Panov & Zykova 2016). This makes them an ideal group for hypothesis testing.

Our study is focused on the research of habitat use and behaviour of two species of agama lizards – *Agama agama* and *Agama weidholzi* that live in sympatry in Southern Senegal.

First of all, it is important to outline what the term sympatry means. It means the coexistence of two related species or populations in the same geographic area (Smith 1969; Mayr 1999; Mallet et al. 2009). Lizards living in sympatry share the same habitat, where they hunt the same preys. The most common differences in the sympatric relationship between species are the use of substrate and prey size (Znari et al. 2000).

Agama lizards (genus *Agama*) are species that have evolved in a variety of environments ranging from tropical forests to dry deserts (Badger 2002, Trape et al. 2012; Panov & Zykova 2016). They are social animals living in groups and colonies (Panov & Zykova 2016; While et al. 2019).

Like other lizards, they need heat, i.e. solar energy, for their activity. Lizards are active mainly in the morning and in the evening. Their activity begins in the morning when the sun is strong enough to warm the substrate. During the day they are hidden to avoid overheating. In the evening they become active again until sunset (Porter & James 1979; Badger 2002; Trape et al. 2012). Typical behaviour of Agama lizards is exhibition of signalling behaviour that is bending of the body and nodding of the head. Another typical behaviour is chasing and fighting (James & Porter 1979; Znari & Benfaida 2001; Trape et al. 2012).

A common anti-predator technique of agama lizards is autotomy which is an ability of a tail self-amputation (Emberts et al. 2019), although the main anti-predator tactic of Agama lizards is quick running (Batabyal et al. 2017; Mikula et al. 2019). The diet of Agama lizards consists predominantly of arthropods (over 60%) with the largest proportion of Diptera and Hymenoptera insects, then plants, seeds, fruits, and animal non-arthropod material (Rabiu 2019; Tan et al. 2020).

The selection of Agama lizard species for this study has been done in accordance with previous observations carried out in Senegal by Joger and Lambert (2002) and Monasterio (2016), and in Gambia by Barnett and Emms (2005). *Agama agama* known as Common/House Agama is a species of lizard found in most of Sub-Saharan Africa. It is commonly known as a well-adapted species of urban areas. The natural habitats are arid zones, mainly stone/shrub semi-desert areas (Uetz 2020a). *Agama weidholzi* is a less known species also called Gambia or Dwarf Agama (Trape et al. 2012; Wilms et al. 2013), it lives in savannah zones of Senegal, Gambia, Guinea-Bissau, Guinea and southern Mali (Wilms et al. 2013; Uetz 2020b).

1.2. Literature Review

1.2.1. Sympatry

In biology, sympatry is explained as an identical occurrence of two related species or populations at the same time in the same place (Smith 1969). That is, the geographical distribution of these two related species or populations overlaps (Mayr 1999). Thus, the overlap area is a range where two related species or populations can potentially live in sympatry (Mallet et al. 2009).

History of the Term Sympatry

The term sympatry was first used and described by E.B. Poulton in 1904 (Mayr 1999; Mallet et al. 2009). In the discussion of the nature of the species he wrote: ‘forms found together in certain geographical areas can be called Sympatric" (Mallet et al. 2009). He also described the opposite phenomenon where species occur separately, dubbed Asympatry (Mayr 1999; Mallet et al. 2009). Later the term Asympatry was changed to allopatry by Ernst Mayr in 1942 (Mayr 1999). Other term parapatry, was later proposed for situations where the ranges of occurrence of two species or populations are in contact and genetic exchange is geographically possible (Mallet et al. 2009). According to Mallet et al. (2009) the contact area is called a contact zone or a hybrid zone.

Sympatric Speciation

The intersection of two species or populations, when they share same area and new species or populations can evolve, is called sympatric speciation (Mallet et al. 2009). The term sympatric speciation is explained by Fitzpatrick et al. (2008) as a contrast between the geographical and demic factors that affect sympatry. These authors suggest that the demic definition is "more accurate" than the geographical definition. They focus more on the flow of genes and selection parameters than on whether speciation is sympatric. Mallet et al. (2009) agree that quantification of gene flow and selection parameters is important for understanding speciation. However, Mallet et al. (2009) question that this purely demic approach cannot explain whether sympatric speciation is (in the original spatial sense) common in nature. According to Mallet et al.

(2009) geographical and strictly demic definitions of sympatric speciation are closely related but not the same.

1.2.2. Sympatry in Reptiles

Many species of lizards are living in sympatry with other lizards. According to Medel et al. (1988) sympatric lizards adapt their patterns of using habitats that they encounter in different parts of their distribution range (mainly similar or related species).

A study of sympatry among lizards from Western Morocco (Znari et al. 2000) points to the distribution of lizard habitats according to their adaptive morphological trails. Rock geckos choose a stone substrate, while some species of skinks or lizards choose gravel, sandy or clay substrate. This study also focuses on the composition of the diet among lizards. There is a great similarity in the taxonomic composition of the diet, in which Formicidae, Isoptera, Coleoptera and Araneidae are predominate, but there is a significant difference in the size of prey eaten by individual species of lizards.

The lizards were observed in the same environment, where they hunt the same prey. The differences in their sympatric relationship are composition of substrate and prey size (Znari et al. 2000).

If all attributes are equal and lizards use resources in the exact same way, interspecific competition can occur (Medel et al. 1988), a process that is generally thought to be the basis for habitat shifts between lizards (Hodges et al. 2007).

1.2.3. Agama Lizards

Agamas are one of the most widespread and diverse groups of Squamata occurring in the Old World, including the African continent. (Leaché et al. 2014). Agama lizards are social animals living in groups and colonies (Panov & Zykova 2016; While et al. 2019). Many Agama lizard species have developed striking sexually dimorphic features, which appear predominantly at the time of mating and include an extravagant colouring of adult males during the breeding season (Leaché et al. 2014). Reproduction of Agama lizards is oviparous (Uetz 2020a; Uetz 2020b).

Distribution of Agama Lizards

The Agama lizards that belong to subfamily Agaminae contain 44 genera and approximately 310 species (Badger 2002; Panov & Zykova 2016). Twenty-three genera are found in mainland Asia, including the Malaysian Peninsula, two in Europe. Another seven genera are limited to the islands of South and Southeast Asia and the continental mainland (Sri Lanka, Malaysia, Philippines). Four genera are found in Africa, two of which are also found in Asia. Eight genera are located in Australia and two of them are present in New Guinea (Panov & Zykova 2016).

The distribution of many species is large, leading to local geographic specialization in many of them (Badger 2002, Trape et al. 2012). If populations are isolated for an extended period of time, they may develop unique features that lead to the creation of new genetic variants (Gonçalves et al. 2018).

Settlement of Agama Lizards in Africa

According to Leaché et al. (2014) the settlement of Agama lizards in Africa was previously associated with the expansion of savanna habitats in Africa at the end of the Miocene. However, Gonçalves et al. (2018) mention that the settlement of new habitats also took place through arid areas.

The Agaminae subfamily most likely colonized Africa from the Arabian Peninsula through semi-arid regions, including the Sahel region (Gonçalves et al. 2018).

Habitats of Agama Lizards

Agama lizards are animals that have evolved in a variety of environments ranging from tropical forests to dry deserts (Badger 2002, Trape et al. 2012; Panov & Zykova 2016). Suitable habitats should provide at least some green matter, although many habitats of agama lizards are dry and therefore do not contain much vegetation. Vegetation, mainly trees and shrubs, also provides suitable shelter. For some of Agama lizard species, the presence of trees is essential. Tropical species are often arboreal and therefore need more green matter to live than desert species that tend to live on rocks (Trape et al. 2012; Panov & Zykova 2016). Due to ever-increasing human development, the Agama lizards find refuge on the walls and ceilings of buildings (Panov & Zykova 2016; Batabyal & Thaker 2019). According to previous observation from Senegal by

Joger and Lambert (2002) agamas were much more abundant in man-made structures than in nature environment.

Morphology of Agama Lizards

Agamas are lizards with well-developed limbs. The hind limbs are always longer and stronger than the front limbs. (Trape et al. 2012; Tan et al. 2020). In general, arboreal species have longer hind legs (Tan et al. 2020). The fingers on the hind limbs are also longer than on the front limbs, the surface of the feet on the hind legs is larger than the front feet (Tan et al. 2020). Blunt head is clearly distinguished from the body (Uetz 2020a). The tail is often as long as the body or even longer with more or less developed autotomy capability (Tan et al. 2020; Uetz 2020a).

Behaviour of Agama Lizards

Agamas as lizards, like other animal groups, show some similar behavioural characteristics that are common to a particular animal group (Barnard 2004).

Day-Time Behaviour

Lizards of the genus *Agama* belong to the diurnal animals (Znari & Benfaida 2001). Lizards are active mainly in the morning and then in the evening. According to Badger (2002), their activity begins in the morning when the sun is strong enough to warm the substrate.

In the morning, they need heat, i.e. solar energy, for their activity. They flatten the body and lie on the ground, as close as possible to the substrate. This enlarges its dorsal surface to increase the area from which they can absorb the sun insolation. At the same time, they will increase their ventral surface to increase the area from which they can collect heat remaining in the substrate (Porter & James 1979).

The lizards are hiding in the shade during the day, when the sun is too strong and could overheat the body (Badger 2002). If they are exposing themselves to the sun, they vertically flatten the body and stand directly against the sun to minimize the area on which the sun falls. They sit in a typical position where the anterior limbs support the body. The body is approximately 30 ° above the surface. The feet and tail touch the ground, while the abdomen does not. Thanks to this, the sun falls mostly on the head and the front of the body (mostly the chest). The rest of the body and tail is overshadowed by the anterior part of the body (Porter & James 1979).

During the evening hours, when the sun is subsiding, lizards are active again (Badger 2002). According to Trape et al. (2012), activity of *Agama agama* continues until the full sunset.

Inter-specific Behaviour

Agama lizards exhibit typical signalling behaviours, when the period of calm (sitting, lying) is interrupted by sets of variously shallow and deep bending of the body and swinging of the head (James & Porter 1979).

This behaviour represents dominance among males who are trying to expel other males from their territories while attracting females. This behaviour is performed only by males. During the active time, males swing intermittently throughout the day. Males swing the body regardless of whether another individual is present in the vicinity or not. Unlike males, females do not perform this body bending or head nodding but perform a specific mouth display when males court them (Znari & Benfaida 2001). According to Carter et al. (2010), the signalling behaviour of males is associated with a higher rate of predation in males than in females.

Another typical behaviour is chasing and fighting. An individual mostly chases the other individual to drive it out of its territory (James & Porter 1979). However, the males also chase or circle the females to try to mate with them (Znari & Benfaida 2001).

Fighting can be seen in males while defending territory (James & Porter 1979). The fight is preceded by ritual behaviour including swinging the body, intimidation, bluffing, etc. If it does not intimidate the opponent, then there is a direct fight where the males bite each other (James & Porter 1979; Trape et al. 2012).

Anti-Predatory Strategies of Agama Lizards

Anti-predatory techniques are the basic behavioural mechanisms of each individual species to avoid predation or other potential threats (Barnard 2004). There are two types of threats. First is avoiding potentially dangerous individuals or groups (in many cases including individuals of their own species). Second is avoiding a possible threat in the form of natural disasters (cyclones, floods, fires, etc.), (Barnard 2004; Batabyal 2017). Every individual tries to optimize its escape strategy by compromising between the benefits of an escape strategy and the cost of the escape (Mikula et al. 2019).

Lizards often change their escape behaviour in urbanized areas due to their habits and the lower risk of predation compared to the natural environment (Mikula et al. 2019).

Cryptic vs Active Species

Some species prefer an active way of life while others prefer to be more hidden. Cryptic species try to merge with their environment to avoid any threats. They use a variety of camouflage techniques. Other anti-predatory techniques are also present. Active species use a wide range of anti-predatory strategies (fast escape, attacking mechanisms etc.). Camouflage is also present in many cases, although it is not as often developed in cryptic species (Lukhtanov et al. 2015).

Running

The main anti-predator tactic of *Agama agama* is a quick escape running (Mikula et al. 2019). According to research by Batabyal et al. (2017) the running is common anti-predatory strategy of most members of Agama lizards. Lizards have longer hind limbs, with wider feet than the front limbs, allowing them for a rapid acceleration and high escape speed. They are predetermined to run, which they use not only to escape, but also to get food or chase other individuals. Agama lizards are highly active. They often run from one place to another for no visible reason (James & Porter 1979; Trape et al. 2012; Mikula et al. 2019).

Autotomy as Unique Tactic

Autotomy is a characteristic anti-predatory feature of many animal taxonomic groups (Emberts et al. 2019; Fernández-Rodríguez & Braña 2020). It is an ability of a self-amputation of a body part (Emberts et al. 2019). Lizards are well-known for tail amputation (Fernández-Rodríguez & Braña 2020). Every Agama lizard species have more or less developed ability for a tail autotomy.

Diet of Agama Lizards

Agamas feed on a variety of invertebrates and small vertebrates. The diet consists predominantly of arthropods (over 60%) with the largest proportion of Diptera (Rabiu 2019) and Hymenoptera insects, especially Formicidae (Tan et al. 2020). Other food includes plants, seeds, fruits, and animal non-arthropod material. Examination of agama lizard diet by age and sex did not show difference in food composition, only in quantity. However, it is possible that there may be differences in the selection of different arthropod species (Rabiu 2019). The differences in diet may also be affected by seasonality and location (Tan et al. 2020).

Agamas are excellent pest controllers. They need to see the movement of prey to detect the prey. They attack their prey at great speed, catch it with a sticky end of the tongue, and then crush it with strong jaws. Agamas are very agile and can catch a fly during its flight (Kraklau 1991; Herrel 1996).

1.2.4. *Agama agama*

Agama agama, called Common Agama or Rainbow Lizard, is a monotypic member of the Agama genus (Badger 2002). It is a large species of its genus, reaching an adult length of 11-26 cm (Uetz 2020a). According to Trape et al. (2012), in Senegal, the male (Figure 1) is characterized by a yellow-green head and a grey-green to olive-green body. The head and body are without stripes and dots. The tail is striped or monochromatic, always with a black tip. Females (Figure 2) and semi-adults are characterized by an olive-green to brown head and body. Females are generally browner. The head is with many stripes and the body is dotted and striped. The tail is often striped with a black tip (Trape et al. 2012). Scales are tiny and keeled. There are large dorsal scale shields on the head (Uetz 2020). In *Agama agama*, temperature-dependent sexual determination was for the first time discovered among reptiles, when gender development is dependent on the external environment temperature. Females are born at lower temperatures than males (Uetz 2020).

Figure 1: Male of *Agama agama*

(Photo by doc. Francisco Ceacero Herrador, Ph.D.)

Figure 2: Female of *Agama agama*

(Photo by doc. Francisco Ceacero Herrador, Ph.D.)

There is some debate concerning the validity of the name *Agama agama* (Linnaeus 1758). The main source of confusion is the lack of samples of types and invalid syntypes. Leaché et al. (2014) suggested using the name *Agama picticauda* for populations found in West Africa. Krishnan et al. (2019) advocated the continued use of *A. agama* for all populations in West and Central Africa and supported the nomenclature according to Linnaeus (1758). In this study, we follow the definition of *A. agama* by Krishnan et al. (2019).

1.2.5. *Agama weidholzi*

Agama weidholzi also called Gambian Agama or Dwarf Agama is a smaller representative of Agama genus. Females have measurements about 56–65 mm and males about 54–62 mm (Uetz 2020b). Males (Figure 3), females (Figure 4), and semi-adults are greyish, green-grey to olive-green. The head of a semi-adult has many lines that gradually fade and disappear in adults. Adult females have typically striped backs, parted by two red parallel lines. Male diamond patterns on the back are less present and two red parallel lines on back are more highlighted than in females (Trape et al. 2012). The tail is longer than the body and is visibly striped at the end. Scales are tiny and keeled. Large scale shields can only be found at the dorsal side of the head (Uetz 2020b).

Figure 3: Male of *Agama weidholzi*

(Photo by doc. Francisco Ceacero Herrador, Ph.D.)

Figure 4: Female of *Agama weidholzi*

(Photo by doc. Francisco Ceacero Herrador, Ph.D.)

1.2.6. Phylogeographic Relationships Among Species

The phylogeographical structure is a product of the life history of the species, its geographical history of species distribution (Hodges et al. 2007). Sympatry takes into account phylogeographical aspects, the overlap of geographical occurrence between species. Therefore, we compare the phylogeographical relationships between the studied species.

Agama agama

There is not yet a well-defined boundary of the *Agama agama* range, it is not exactly defined by IUCN. There are several documented evidence-based occurrences of this species. According to Uetz (2020a), *Agama agama* is found in Benin, Burkina Faso, Cameroon, Cape Verde, Chad, Ghana, Guinea (Conakry), Guinea-Bissau, Liberia, Mali, Mauritania, Nigeria, Senegal, Togo, Ivory Coast and Gabon.

Agama weidholzi

Agama weidholzi is found in Gambia; Senegal, Guinea; Guinea-Bissau and west part of Mali (Wilms et al. 2013; Uetz 2020b).

The occurrence of *Agama weidholzi* completely overlaps with the occurrence of *Agama agama*. Hypothetically, *Agama agama* can be always present on the territory of *Agama weidholzi*. Sympatry between species can always occur.

2. Aims of the Thesis

The goal of this diploma thesis is to analyse the spatial and behavioural segregation of selected Agama lizard species, and to find out similarities and differences in habitat use and behaviour under sympatric conditions.

2.1. The Hypothesis

The differences in sympatric relationship between lizards are in the use of substrate and prey size (Znari et al. 2000). Medel et al. (1988) mentioned the difference between similar or related sympatric lizards is also in the using of different parts of habitats.

In this study, we do not focus on prey size, but on spatial segregation, which also involves substrate selection and using of different parts of habitats.

Due to the fact that the studied species are similar and related to each other, we assume that there is no segregation in the substrate, but only in the use of different parts of the habitat.

1.H_0: The null hypothesis assumes segregation only in the use of different parts of the habitat.

1.H_1: The alternative hypothesis assumes a higher degree of segregation, not only in the use of different parts of the habitat, but also in the occupation of different substrates (different types of habitats).

According to Batabyal et al. (2017) and Mikula et al. (2019) the running is common anti-predatory strategy of most members of Agama lizards (demonstrated in *Agama agama*).

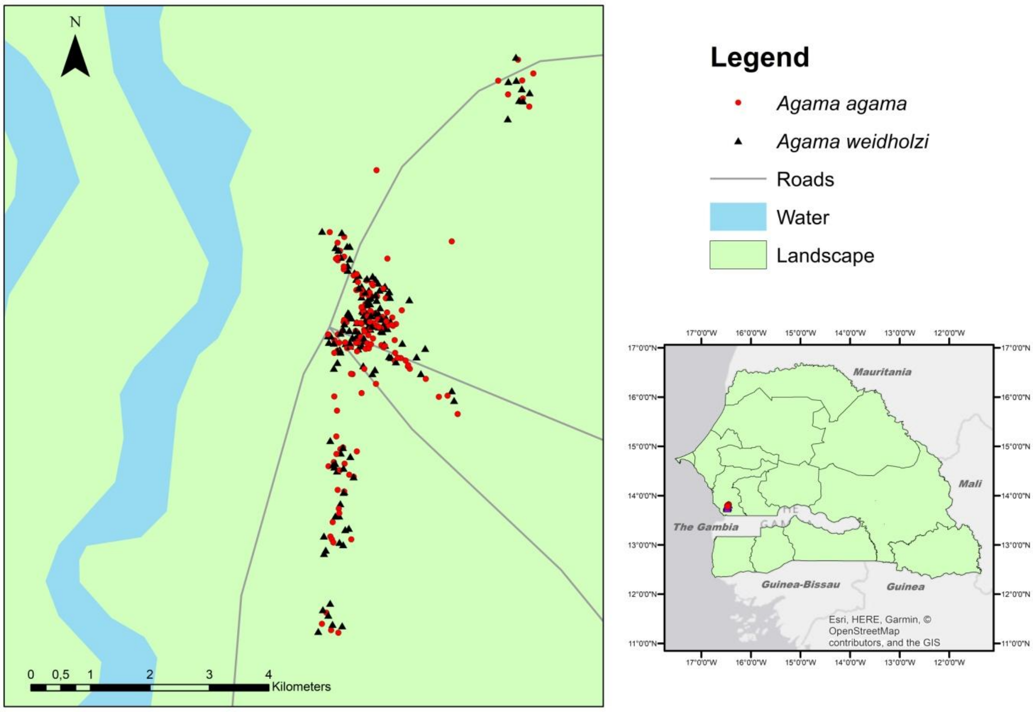
2.H_0: The running is common anti-predatory strategy of both species.

2.H_1: The running is common in *A. agama*. *A. weidholzi* prefers different anti-predatory strategy.

3. Methods

The study was conducted in October 2018 in Toubakouta town in Senegal (latitudes 13°65'N and 16°46'W), shown in Figure 5. We observed 325 individuals in total, from which 154 individuals belonged to *Agama agama* and 171 individuals to *Agama weidholzi*.

Figure 5: Study Area



(Resources: own processing according to ArcGIS – version 10.4.)

3.1. Description of the Observation Site

Toubakouta Town

Toubakouta town is located in the central-western part of Senegal in Fatick region. The town lies in the Delta of Saloum River, 15 km west from the Atlantic coast, 23 km north from Karang town (Gambia border) and 70 km southwest from the capital of the Fatick region named Kaolack. The area of the town is circa 1.2 km^2.

Climate Condition

In Senegal, the climate is affected by two annual cycles, the dry season, and the rainy season. The dry season takes place from November to April. The rainy season is occurring from May to October. Data for the study were collected in October 2018, in the end of the rainy season, when the precipitation is gradually decreasing and the temperature starts to rise. The temperatures range from 23°C to 32°C in October (Climates to travel 2020).

Ecosystem Patterns

Savannah is a typical habitat for the southern part of Senegal (Convention on Biological Diversity 2020), where Toubakouta lies. The town of Toubakouta is located directly in the delta of Saloum River, thus being a place with a large reservoir of water even in the dry season. Toubakouta is surrounded by bushes with the majority of acacia trees from the north and east. Open savannah is present in the south of the town. Due to the presence of blast water in the delta of Saloum River, mangrove vegetation is present in the west of the town.

3.2. Field Monitoring

The study was conducted from 8th to 23rd October 2018 in Toubakouta town, surrounding nature areas and surrounding villages (Soukouta, Sangako, Bani, Sourou, Dassilame Serere and Nema Ba). Practical fieldwork was conducted as daily field monitoring due to the fact that diurnal animals were being subjects of the observation.

The observation of animals was divided into tracks to ensure statistic continuality of observation. One track consisted of three hours monitoring. There were 2-3 tracks per day (depending on the weather) to cover the whole daylight hours. The first track was happening in the morning or an early hour, the second track took place at noon or in the afternoon, the third track in the evening. There was no monitoring done on 12 October because the GPS device did not work and had to be replaced and for this reason only one evening observation was made on October 13. Altogether, 31 tracks were performed.

3.3. Data Collection

A visual observation method was used for the study. Field monitoring for data collection was performed by sight or binocular. The collected field data were recorded on a paper sheet. GPS coordinates of every observed individual and tracks were registered by Geo tracker.

The following variables were collected for statistical analysis: number of track, waypoint, GPS coordinates, date, time of observation, species name, sex, microhabitat, presence and size of vegetation in the microhabitat, escaping direction, level of rain and cloudiness. If more animals were present at one waypoint, the distance between them was recorded. If there was a concrete structure in the habitat, a height, a colour and other descriptive details (gaps, roof) were taken note of as well as the height at which animal occurred on the structure.

Temperature and air humidity were not recorded because its variability during the study period was extremely low. However, the temperature is mentioned in the occupation of the top of the concrete structure, which is the most suitable part of the concrete structure for basking.

3.4. Data Processing

The data were transcripted to an Excel file with added attributes. These are whether the animal was found on man-mad structure or in natural habitat and substrate of the surface on which the animal occurred was added. In case of concrete structures, it was calculated at which proportional height the animal occurred on the wall. The GPS coordinates of the waypoints were typed into the Geographic Information System (GIS), where they were further processed. A GIS map layer with coordinates of all observed animals was created. The layer is represented as a set of dots that stands for all observed animals. The distance between the animals was calculated using a measuring tool. Four distances were recorded from each animal to the closest *A.agama*-male, *A.agama*-female, *A.weidholzi*-male, *A.weidholzi-female*. The distances were transcripted to Excel file.

3.5. Statistical Analyses

Analyses of processed data were performed in IBM© SPSS© Statistics (version 25.0 for Windows; IBM, USA). The variables used in each analysis are recorded in italics. Kolmogorov-Smirnov tests were used to detect normality for the continuous variables recorded, in order to apply the subsequent statistical approach.

Binary tests were used to detect variations from hypothesized equal distributions in the variables studied within each species, while χ^2 tests showed differences in these same variables between species.

Niche selection of *A. agama* and *A. weidholzi* was determined through ANOVAs which was used for interspecific and sex class differences in *size of concrete structures, high of concrete structures* and *size of vegetation in habitat*. Fisher test was used to calculate interspecific differences in *size of populations, sex ratio, artificial/natural habitat, substrate, using of top of the structures, structures with holes, roofed structures, comparing of escape directions*. Tukey post-hoc test was used for calculation preferences for basking on top of walls (occupying top of walls), where $\chi 2$ was used to detect differences in interspecific and sex class differences. Man-Whitney test was used to determine differences in activity due to *Cloudiness*.

Escape tactics between species and sex classes were tested through $\chi 2$. Subsequently, Categorical Principal Component analysis (CPA) was used to plot niche selection variables like *Structure_Size*, *Vegetation_Size*, *Substrate*, *Metallic_Roof*, *Top_of_Wall*, and *Kind_of_Wall* together with *SpSex* and *Escape* as supplementary variables, in order to detect links between the niche selection and the escape tactic.

Neighbouring preferences were studied in two ways: ANOVAs were used to detect differences in average distances found between each species and sex classes, χ^2 was used to determine interspecific preferences for keeping the same or the sympatric species as the closest neighbour, as well as to assess intraspecific preferences for keeping conspecifics from the same or different sex as the closest intraspecific neighbour. Each interindividual distance indicated the average distance observed between a given species and sex class and the closest individual of any other species and sex class.

The analysis of animal´s occurrences on piles of concrete structures was not performed due to the low occurrence on piles of concrete blocks (22 individuals – 9 individuals of *Agama agama* and 13 individuals of *Agama weidholzi*).

Comparison of occurrence on roofed walls with escape directions was not performed due to the low number of such occurrences (28 individuals on roofed walls), the result would be statistically insignificant. No analysis has been performed.

No rain was recorded for the entire study period. When it rained, it was always a heavy rain (100% rain) and no observation took place during such times. For this reason, 0% of rain is noted for all observed individuals and no further calculation was conducted.

4. Results

4.1. Structure of the populations

Population size

I observed 325 individual animals in total, 154 were *Agama agama* and 171 belong to *Agama weidholzi*. 47.38% of observed individuals were *A. agama* and 52.62% were *A. weidholzi*. These proportions do not differ from the equal proportion hypothesized (B=0.888, n=325, p=0.375) and thus, both species show similar population size.

Sex ratio

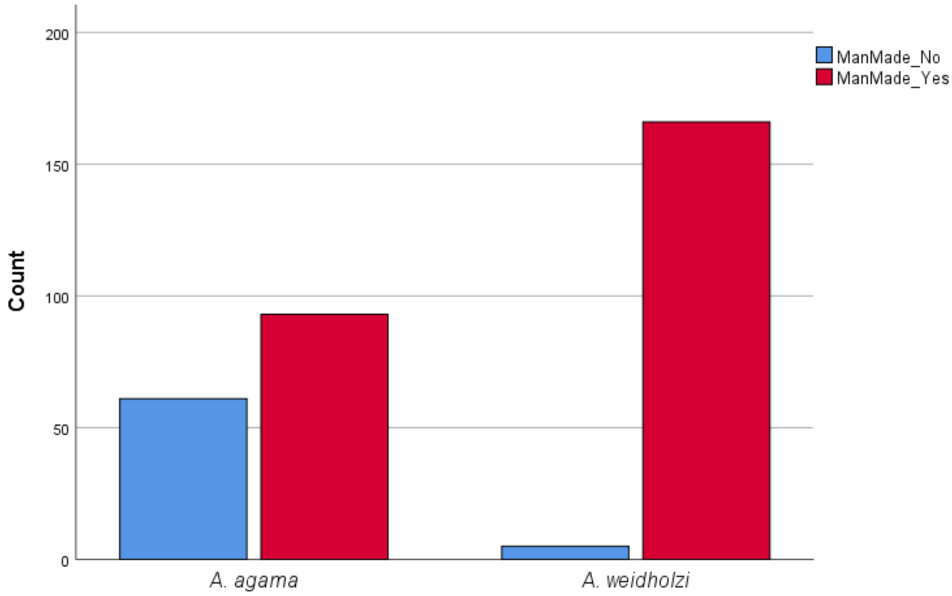
The percentage breakdown by sex of all the observed individuals is: 24% *A. agama*-male, 21.85% *A. agama*-female, 1.54% unidentified *A. agama*, 20% *A. weidholzi*-male, 20.31% *A. weidholzi*-female and 12.31% unidentified *A. weidholzi*. For both species the sex ratio detected was not different from the 1:1 hypothesized (*A. agama*: B=0.492, n=149, p=0.623; *A. weidholzi*: B=0.001, n=131, p=1.000).

4.2. Niche Selection

Artificial vs Natural Habitats

In *A. agama,* 93 individuals (60.39%) were found on man-made structures and 61 (39.61%) in natural habitats; that means a significant preference for man-made structures in urban habitats (B=2.498, n=154, p=0.012; Figure 6). In *A. weidholzi*, 166 individuals (97.08%) were found on man-made structures and only 5 (2.92%) in natural habitats; that also means a significant preference for man-made structures (B=12.236, n=171, p<0.001). Both species showed segregation in terms of use of these habitats (χ^2=67.386, p<0.001), since the preference for man-made habitat was much stronger in *A. weidholzi*.

Figure 6: Artificial vs Natural Habitats by Species



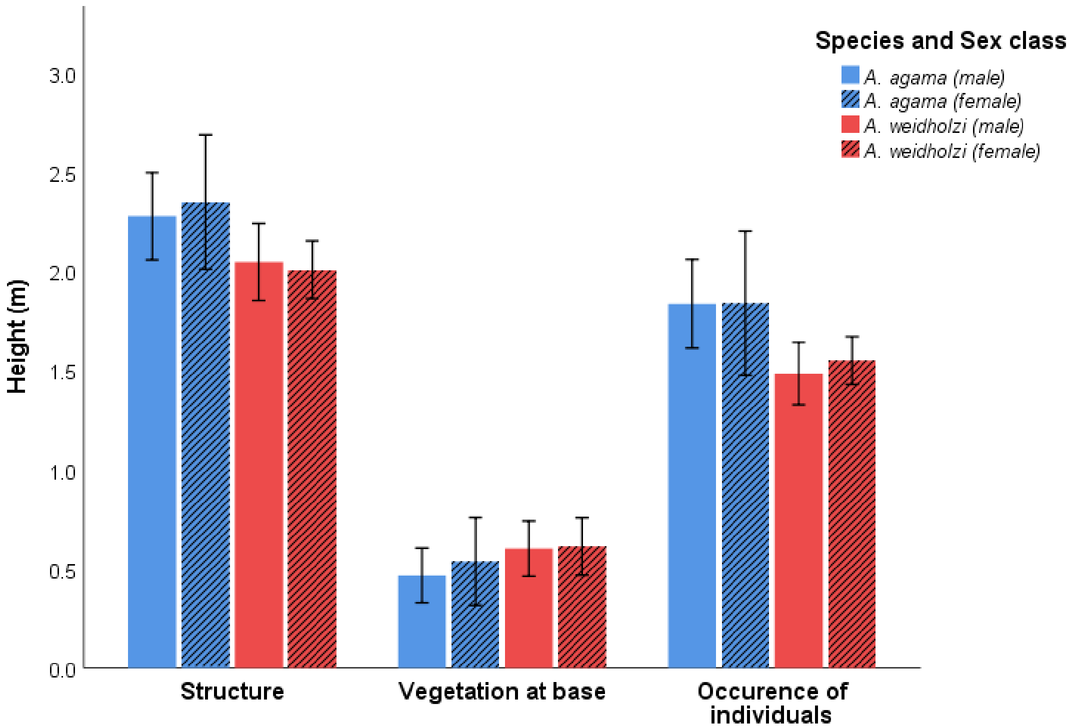
(Resources: own processing according to Statistics - version 25.0)

Consequently, while 38.31% of the individuals of *A. agama* were observed on trees, only 2.34% of *A. weidholzi* individuals were observed in that substrate. Since the natural habitats are clearly dominated by *A. agama*, we will not further analyse the natural habitats, but we will focus in the commonest sympatric habitat of both species: concrete structures represented by walls and piles of concrete bricks.

Height of the Structures

The average wall height where *A. agama* individuals were found was 2.327 ± 0.864 m, but 2.039 ± 0.669 m for *A. weidholzi* which was significantly lower (F=8.838, n=256, p=0.003; Figure 7). However, no differences were found in height of selected structures between sexes neither for *A. agama* (F=0.118, n=89, p=0.732) nor for *A. weidholzi* (F=0.100, n=125, p=0.752).

Figure 7: Niche Selection Selected by Each Sex within Each Species



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Height of Occurrence of Individuals

Both species selected a similar relative height within the structure: 81.8 ± 24.9% of the wall height for *A. agama*, and 77.50 ± 23.7% for *A. weidholzi* (F=1.821, n=256, p=0.178). However, since *A. agama* choose higher walls than *A. weidholzi*. *A. agama* was observed basking at greater height than *A. weidholzi* (1.795 ± 0.939 m *vs*. 1.484 ± 0.582; F=13.164, n=325, p<0.001; Figure 7). Both sexes had similar niche selection in terms of height within each species (*A. agama*: F=1.131, n=149, p=0.289; *A. weidholzi*: F=1.459, n=131, p=0.229).

Use of the Top of the Structures

Forty-three individuals of *A. agama* (48.86%) and 57 of *A. weidholzi* (34.76%) were observed basking on the top of the walls. The selection of this resource was significantly different between both species (Table 1). However, the use of this resource was similar between sexes within each species, although a non-significant tendency for greater use of the top of walls by males was observed in both species.

Table 1: Preferences for Basking on Top of Walls by Male and Female Individuals of *Agama agama* and *Agama weidholzi*.

	Top	Not-on-top	
Agama agama	47.3%	52.7%	χ^2=3.979, n=256, p=0.046
Agama weidholzi	34.5%	65.5%	
A. agama ♂	50.0%	50.0%	χ^2=3.316, n=91, p=0.191
A. agama ♀	38.7%	61.3%	
A. weidholzi ♂	44.3%	55.7%	χ^2=4.079, n=156, p=0.130
A. weidholzi ♀	28.1%	71.9%	

(Resources: own processing according to Statistics - version 25.0)

Use of Structures with Holes

Fifty-three individuals of *A. agama* (60.23%) and 103 individuals of *A. weidholzi* (62.80%) were sighted on walls or piles of concrete blocks with gaps. These proportions are not different between species (χ^2=0.431, n=256, p=0.300). Similarly, the selection of structures with holes was not different between sexes neither for *A. agama* (χ^2=1.474, n=91, p=0.593) nor for *A. weidholzi* (χ^2=0.426, n=165, p=0.840).

Selection of Walls with Roofs

Out of 230 individuals found on the walls, 28 individuals were on the walls with a roof and 202 were observed on the walls without a roof, including 22 individuals found on piles of concrete blocks. Among the individuals found in walls with roof, 17 were *A. agama* (21.52%) and 11 were *A. weidholzi* (7.28%). The preference for such kind of structures was significantly different between both species (χ^2=11.814, n=235, p=0.001). The overall low selectivity for this kind of structures did not allow to analyse differences by sex.

Presence or Absence of Vegetation

Preference for walls with basal vegetation was significantly higher in *A. weidholzi* (79.53%) than in *A. agama* (55.84%; χ^2=22.234, n=322, p<0.001). Within each species, the preference for walls with basal vegetation was not different between sexes neither in *A. agama* (χ^2=5.138, n=151, p=0.072) nor in *A. weidholzi* (χ^2=0.725, n=171, p=0.716).

Height of Vegetation

A. agama individuals were observed in walls with an average vegetation height of 0.344 ± 0.479 m, while it was 0.605 ± 0.569 m for *A. weidholzi*, significantly higher ($F=19.502$, $n=322$, $p<0.001$; Figure 7). Considering species and sex, Tukey test detected that vegetation height in the selected walls was low for *A. agama* females (0.313 m), low-average for *A. agama* males (0.376 m), average-high for *A. weidholzi* males (0.575 m), and high for *A. weidholzi* females (0.608 m).

4.3. Behavioural Differences

Escape directions

The directions of escape were recorded for each individual (Table 2) and were significantly different between both species ($\chi^2=69.536$, $n=317$, $p<0.001$). *A. agama* tends to escape predominantly upwards, but escape to the other side of the wall is also common. On the contrary, *A. weidholzi* tends to escape downwards, and escaping upwards and to the other side of the wall are also significantly observed.

Table 2: Recorded Escape Directions by Species

	Other side	Upwards	Straight	To gaps	Downwards	Unknown
A. agama	28	91	9	10	8	7
A. weidholzi	39	42	4	15	69	1

(Resources: own processing according to Statistics - version 25.0)

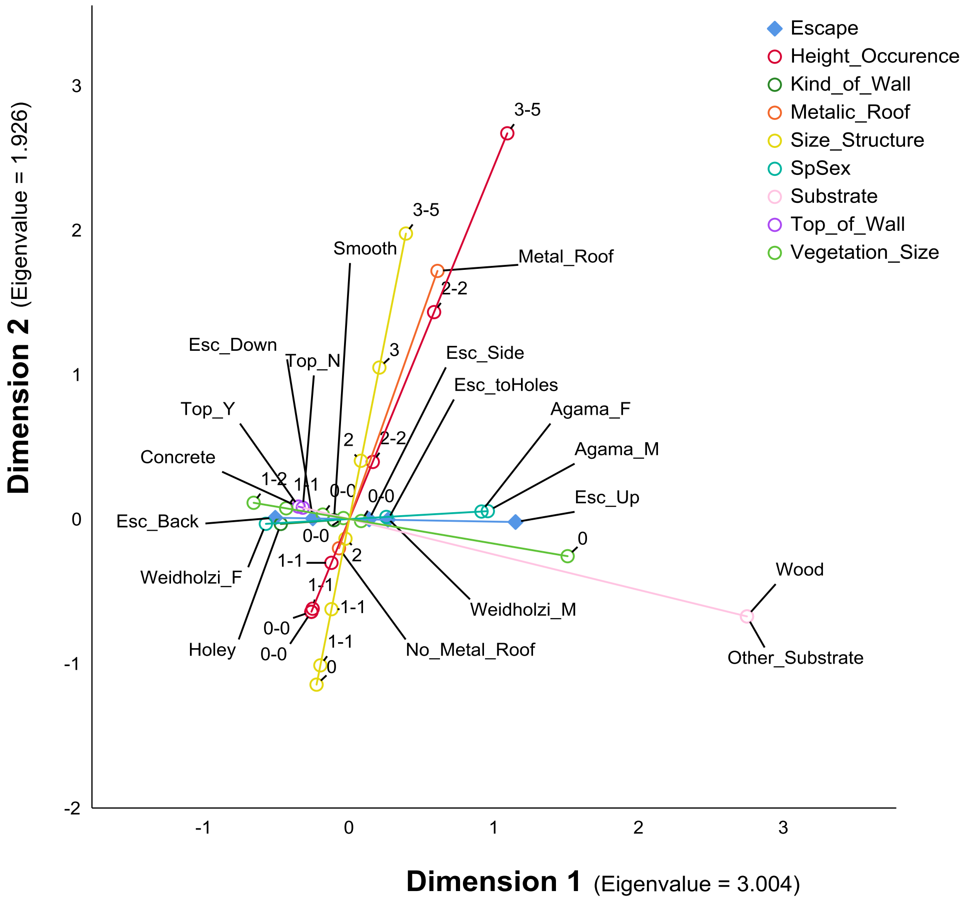
Escape behaviour was different between sexes in *A. agama* ($\chi^2=25.251$, $n=147$, $p=0.006$) with higher preference for males to escape to the other side, but to escape upwards by females. However, escape behaviour was the same for males and females of *A. weidholzi* ($\chi^2=13.077$, $n=170$, $p=0.104$).

Influence of Niche Selection on the Escape Direction

Categorical Principal Component analysis (CPA) was used to plot niche selection variables (*Structure_Size*, *Vegetation_Size*, *Substrate*, *Metallic_Roof*, *Top_of_Wall*, and *Kind_of_Wall*) together with *SpSex* and *Escape* as supplementary variables, in order to detect links between niche selection and escape tactic.

The CPA (Figure 8) showed that upwards escape tactic was linked to *A. agama* and structures without vegetation at the base, mainly trees. On the contrary, the escape tactic downwards or to the other side of the structure was associated with smooth concrete walls with high vegetation at its base. Both tactics were not connected to the height where the animal was detected and the height of the structure.

Figure 8: Categorical Principal Components Analyses Showing the Connections between Niche Selection and Escape Tactics by Male and Females of *Agama agama* and *Agama weidholzi*



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Escaping to the other side of the wall (when the animal was basking in the top) is also frequent in both species (Table 3). On the contrary, side movements or escaping to hideouts (holes) was scarcely used by both species.

Table 3: Escape Preferences of Male and Female Individuals of *Agama agama* and *Agama weidholzi*

	Top	Not-on-top	
Agama agama	47.3%	52.7%	n = 256, χ^2 = 3.979, p = 0.046
Agama weidholzi	34.5%	65.5%	
A. agama ♂	50.0%	50.0%	n = 91, χ^2 = 3.316, p = 0.191
A. agama ♀	38.7%	61.3%	
A. weidholzi ♂	44.3%	55.7%	n = 165, χ^2 = 4.079, p = 0.130
A. weidholzi ♀	28.1%	71.9%	

(Resources: own processing according to Statistics - version 25.0)

4.4. Spatial Segregation

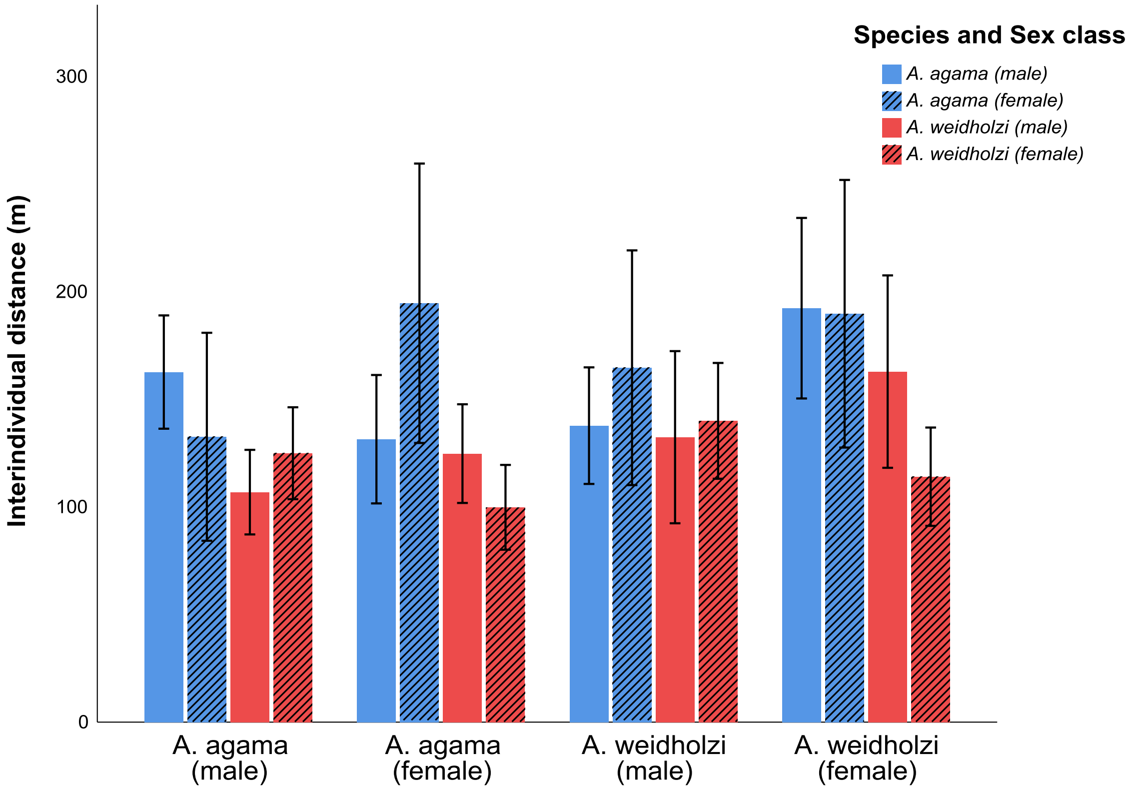
Neighbouring Preferences

We calculated the distance between every individual of a given species and sex class with the closest individual of other species and sex class, that is, with the closest male of *A. agama* and *A. weidholzi* and the closest female of *A. agama* and *A. weidholzi*. Neighbouring preferences were studied by ANOVAs (differences in the average distances between individuals) and χ^2 (interspecific and intraspecific distance preferences).

A. agama tended to keep more distance to its closest neighbour than *A. weidholzi* for most combinations (*A. agama* ♂: 148.6 ± 13.0 m *vs*. 117.3 ± 6.5 m; n=325, F=4.901, p=0.028); (*A. agama* ♀: 160.8 ± 17.0 m *vs*. 113.6 ± 6.7 m; n=325, F=7.153, p=0.008); (*A. weidholzi* ♀: 191.8 ± 18.4 m *vs*. 137.4 ± 10.7 m; n=325, F=6.847, p=0.009), except *A. weidholzi* ♂ (152.6 ± 14.9 m *vs*. 135.9 ± 10.4 m, n=325, F=0.876, p=0.350). However, interesting different patterns between males and females appeared in both species. Males of *A. agama* kept females of both species at similar distance but closest conspecific males much farther than those of *A. weidholzi* (Figure 9; n=279, F=2.233, p=0.085), while females showed opposite pattern keeping closest males of both species at similar distance but closest conspecific females much further than those of *A.*

weidholzi (n=279, F=4.133, p=0.007). Males of *A. weidholzi* kept closest individuals of each species and sex combination at similar distance (n=279, F=0.549, p=0.649); however, females kept female conspecifics closer that other species and sex combinations (n=279, F=2.491, p=0.061).

Figure 9: Neighbouring Preferences by Males and Females of *Agama agama* and *Agama weidholzi*



(Resources: own processing according to Statistics - version 25.0)

Indeed, χ^2 tests showed that males of *A. agama* selected females as preferred closest intraspecific neighbours, while females preferred males. On the contrary, males of *A. weidholzi* selected other males as preferred closest interspecific neighbour, while females tended to prefer other females (Table 4).

When it comes to the interspecific neighbouring, no significant pattern was found although both species tended to prefer individuals from the same species as closest neighbours (Table 4). Both species do not show significant differences in the preference of presence of their own species over the other or vice versa (Table 4).

Table 4: Neighbouring Preferences by Male and Female Individuals of *Agama agama* and *Agama weidholzi*

	Intraspecific closest		Interspecific closest	
	♂	♀	*A. agama*	*A. weidholzi*
Agama agama	52.6%	47.4%	52.6%	47.4%
Agama weidholzi	46.2%	53.8%	46.8%	53.2%
	n = 325, χ^2 = 1.327, p = 0.249		n = 325, χ^2 = 1.096, p = 0.295	
A. agama ♂	37.2%	62.8%	48.7%	51.3%
A. agama ♀	71.8%	28.2%	57.7%	42.3%
A. weidholzi ♂	53.8%	46.2%	40.0%	60.0%
A. weidholzi ♀	42.4%	57.6%	47.0%	53.0%
	n = 280, χ^2 = 20.444, p < 0.001		n = 280, χ^2 = 4.373, p = 0.224	

(Resources: own processing according to Statistics - version 25.0)

4.5. Activity Patterns

Cloudiness

The level of cloudiness was recorded for each observation, and then averaged for each species. For *A. agama* the average cloudiness was 28%, and 29% for *Agama weidholzi*, with no significant difference (U=13766, n=325, p=0.475). No differences in activity patterns related to cloudiness were found neither among the species (U=13766, n=325, p=0.475), nor between sexes within each species (*A. agama*: U=2387, n=149, p=0.143; *A. weidholzi*: U=2151, n=131, p=0.978).

4.6. Summary of Similarities and Differences between Species

The number of analyses (Table 5) where the species show similarities (insignificant difference) is 8. The number of analyses where the species show differences (significant difference) is 6. The total number of statistical analyses is 14.

Table 5: Similarities and Differences between *Agama agama* and *Agama weidholzi* Living in Sympatry in Southern Senegal.

Studied trait	***Agama agama***	***Agama weidholzi***
Population Size	Insignificant difference	
Sex Ratio	Insignificant difference	
Artificial vs Natural Habitat	Less artificial	More artificial
Height of the Structure	Insignificant difference	
Height of Occurrence of Individuals	Insignificant difference	
Use of the Top of the Structures	More	Less
Use of Structures with Holes	Insignificant difference	
Selection of Walls with Roofs	More	Less
Presence or Absence of Vegetation	Absence	Presence
Height of vegetation	Lower	Higher
Escape directions	Upwards	Downwards
Influence of Niche Selection on the Escape Direction	Insignificant difference	
Neighbouring Preferences	Insignificant difference	
Cloudiness	Insignificant difference	

(Resources: own processing)

5. Discussion

The results indicate that the number of observed similarities is higher than the number of observed differences between the species under sympatric conditions. The results suggest that *Agama agama* occurs in both man-made and natural habitat while *Agama weidholzi* occurs almost exclusively in man-made habitat. In man-made habitat, *A. agama* more prefers to occupy the tops of walls and roofed walls compared to *A. weidholzi*. *A. agama* does not choose habitat according to the presence of vegetation. If vegetation is present, the height of vegetation is lower than for *A. weidholzi*. The escape direction is mostly upwards. *A. weidholzi* tends to inhabit places with the presence of vegetation. The height of vegetation is more prominent than in case of *A. agama*. The escape direction is mostly downwards, but there are also significant cases of escapes upwards and to the other side of the wall.

The analyses confirm the fulfillment of the first alternative hypothesis ($1.H_1$) when a degree of segregation lies not only in the use of different parts of the habitat, but also in the occupation of different substrates (different types of habitats). *Agama agama* tends to occupy man-made structures, that are represented by concrete structures, but significant part of population lives in natural habitat, represented mainly by trees (wood substrates). *Agama weidholzi* almost exclusively occurs in man-made structures (concrete walls).

Contrary to the first null hypothesis ($1.H_0$), both species do not show big differences in terms of using different parts of the habitat. The species use similar size of concrete structures. The height of occurrence on concrete structure is also similar. Both species do not prefer concrete structures with presence of holes. The differences can be seen in using of top of structures and roofed structures, when *Agama agama* tends to occupy top of structures and roofed structures more frequently than *Agama weidholzi*.

The data suggest that the spatial differences between *A. agama* and *A. weidholzi* under sympatric conditions are more in using different types of habitats (different types of substrate) than in using different parts of the habitat.

In terms of behavior, we can confirm the second null hypothesis ($2.H_0$) and support claims of Batabyal et al. (2017) and Mikula et al. (2019), the running is common anti-predatory strategy of Agama lizards, which was observed in both studied species. Interspecies differences were observed in the escape directions.

The identification of correlations, patterns and relationships between the data indicate that there is no interspecific difference between the two observed species and therefore both sexes do not show significant differences in spatial segregation, escape direction or neighboring preferences within both studied species.

We can confirm claims of James and Porter (1979), Znari and Benfaida (2001), and Trape et al. (2012) that Agama lizards show typical signaling behavior - clicking, as well as chasing and fighting, that were observed in both species during fieldwork, but due to the small number of observed samples, those were not part of statistical analyses but taken into account in discussion.

In case of differences in spatial segregation and escape directions, a tendency of *Agama weidholzi* is to escape predominantly downwards and to prefer habitat with presence of vegetation and larger size of vegetation compared to *Agama agama* can be supported by the observation during fieldwork, when a small hawk, probably *Accipiter nisus*, *ovampenis* or *badius* (IUCN 2020) was seen attacking an adult *Agama weidholzi* who managed to escape down the wall into the vegetation. The hawk was as big as a Common kestrel. The other agama species, *Agama agama* measures about 15–25 cm and it is therefore too big of a prey for it. That may be why *Agama agama* probably does not see a threat in a hawk and therefore tends to escapes upwards. The real threats to the *Agama agama* species are monitor lizards, dogs, and humans in the local environment. Although according to IUCN (2020) there may be larger bird predators, only smaller raptors of Accipiter and Milvus genus were observed. Probably for this reason, *Agama agama* does not perceive aerial bird predators as a thread compared to *Agama weidholzi*, which is smaller in size and therefore is more suitable food for more kinds of predators. This theory, however, would need further research.

The results confirm that agama lizards are synanthropic and thrive in human presence. During fieldwork, a large numbers of livestock have been observed in human settlements, and garbage, which goes hand in hand with a growing human population, attracts insects. This creates an almost inexhaustible source of prey for agamas. Agamid lizards therefore have a preference towards human environment rather than natural habitats, which support the theories of Joger & Lambert (2002) and Panov & Zykova (2016).

The study demonstrates a correlation between studied species in terms of spatial and behavioral segregation under sympatric conditions in Southern Senegal. These results build on existing evidence of species *Agama agama*. In the case of the species *Agama weidholzi*, these are unique results that take into account the spatial and behavioral segregation of this species. This research could be used as a comparative study for further observations of *Agama weidholzi*. The results of this study are unique because they provide a new insight into the relationship between the observed species under sympatric conditions that have not yet been observed between these species. The data contribute to a clearer understanding of the sympatry between similar and related Agama lizard species. These results should be taken into account when considering spatial and behavioral segregation among sympatric lizards, mainly in case of agamous lizards.

The generality of the results is limited by the size of the observed sample (325 individuals - 154 individuals were belonging to *Agama agama* and 171 individuals to *Agama weidholzi*). Methodological decisions were limited during practical fieldwork, when there was a partial change in the content and scope of the study depending on local conditions. Prior to the observation, the individual tracks were designed so that their sections did not overlap with other tracks, so that there was no individual counted repetitively. However, the agamas are mobile and therefore there may have been duplications in some of the individuals. A higher number of individuals with unidentified sex in *Agama weidholzi* than in *Agama agama* is caused by more difficult sex differentiation field monitoring of *A. weidholzi* compared to *A. agama*. The reliability of these data may be also affected by seasonality and local geographical conditions. It is beyond the scope of this study to assess whether sympatry between observed species occurs only spatially or whether gene exchange occurs. Gene analysis would be needed here.

Further research on the sympatry between *Agama agama* and *Agama weidholzi* in other localities is needed to compare the outcome of this study and to extend information about these species, mainly in the case of *Agama weidholzi*, which has not yet been the subject of any scientific study.

6. Conclusions

Both species show similar population size and sex composition. In niche selection, the species use similar size of concrete structures. The height of occurrence on concrete structure is also similar. Both species do not prefer concrete structures with presence of holes. The studied species do not show a significant difference in the influence of niche selection on escape directions. Insignificant differences between the studied species were also found out in spatial segregation and activity pattern, including cloudiness.

Significant differences between the studied species were analyzed in niche selection and escape directions when *Agama agama* occurs in artificial habitat and natural habitat while *Agama weidholzi* almost exclusively inhabits artificial habitat. *A. agama* prefers to occupy the tops of walls and roofed walls rather than *A. weidholzi*. *A. agama* does not choose habitat according to the presence of vegetation. If vegetation is present, the height of basal vegetation is lower than for *A. weidholzi*. The escape direction is mostly upwards. *A. weidholzi* tends to occur in places with the presence of vegetation. The height of basal vegetation is higher than for *A. agama*. The escape direction is mostly downwards, but there are also significant incidences of escapes up and to the other side of the wall.

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