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Some aspects of nest digging and egg laying behaviour in the arboreal agamid lizard, *Agama atricollis* Smith 1849 (= *Acanthocercus atricollis* Smith 1849)

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DETAILS of nest digging and egg laying behaviour in agamids are poorly documented in the literature, partly due to the secretive behaviour of the female, but also due to the care taken to camouflage the nest. Cott (1934, 1957) and Loveridge (1953) refer to the concealing and often cryptic coloration of *Agama atricollis*, which made them very difficult to see in the natural state. A description of nest digging behaviour in oriental agamids has been reported by McCann (1937) and Taylor (1951). Fitzsimmons (1943), in his description of some South African lizards, reported on the egg laying habits of *Agama atra*. The female was stated to have laid eggs one by one and carefully covered each with sand until the hole was filled in. Harris (1964) gave a detailed description of egg laying in the African agamid, *Agama agama*. The nest digging and egg covering behaviour of this lizard and *Agama atricollis* appear to be the same but they differ in their behaviour during egg laying. *Agama agama* is reported to straddle the nest during egg laying, to remain motionless with tail erect and head up, and to inspect each egg after laying. The account which follows gives a detailed description of nest digging, egg laying and the subsequent camouflage of the nest in *Agama atricollis*, based on a PhD study conducted between September 1968 and December 1973 (submitted 1976). Since the type specimens of *Agama atricollis* were identified by staff at the Natural History Museum in London (BMNH), this name will be retained in this study, and the recent name changes will be bracketed.

Agama atricollis is essentially an arboreal lizard confined to the tropical grassland-scattered woodland vegetation belts of east and southern Africa. At Kisumu (Kenya) the lizard was associated with certain features of the habitat, notably trees within the study area and the ground between them. Both the male and female lizards are territorial. In the study area, the ecological requirements were considered by an examination of the two main features of the habitat selected for daily activity, namely, those on the ground and those above ground level. Analysis of the daily activities suggest that the maintenance requirements like food, suitable temperature and rest, are attained by the provision of trees, hedges, and bushes which provide basking and resting facilities for these lizards. In addition it is from such sites that the lizard is able to observe prey on the ground and above ground. Trees, bushes and raised structures like fence posts provide vantage points which enable a lizard to keep an eye on other lizards, and to display its presence to other conspecifics of either sex to the full. Nest construction egg laying and incubation require soil, if the entire reproductive effort is to be maintained.

The Study Area

The main study area was centred at Kisumu, a town in Kenya, situated 0 .06S and 34.45 E, on the NE shores of the Kavirondo Gulf of Lake Victoria (Figure 1). In altitude it extends from 1,135 m on the Kavirondo Gulf shore to 1,146 m in the town itself. The areas where this study was made were all much disturbed by man. Those areas on which I concentrated were artificial gardens on the Kisumu Boys High School compound, roadside hedges and trees. The area chosen was covered with stone buildings, pathways and playing fields. Trees of *Jacaranda*, *Cassia*, *Delonix*, *Allamanda* and *Markhamia* species are planted at fairly regular intervals along the main tracks and the edges of the compound. Ornamental shrubs and hedges line the paths. The Kisumu area falls within Ecological Zone III, as defined by Pratt *et al*. (1966) with a climate from dry to sub-humid to semi-dry. Sunshine hours, rainfall and temperature

for Kisumu for a 40 year period, is shown in Figure 2. Diurnal variations for temperature are in the range 7–9°C. Kisumu is situated in an area with at least some rain throughout the year, with peaks from March to June (long rains). A slightly smaller rainfall peak occurs in August.

METHODS

Binoculars of magnification 8 x 30 were used for observation in the field. Details of actual nest construction, egg laying and post depositional behaviour were observed and recorded on film, both cine and still and in note form. Many 'observed nests' were dug up using both hard and soft bristle brushes, so that data on nest dimensions, shape, the number of eggs and egg arrangement, could be obtained. All sites were observed daily. Eggs were put back into the nest after weighing and covered with soil. Every tree in the area studied had painted half metre height marks from the base to six metres up its trunk, so that the vertical distance up the tree at various times of the day could also be measured. At the same time temperature measurements were taken of the immediate environment using an automatic Grant Thermister recorder. The temperature of the substratum and shaded air temperature one, two and six metres above ground level was measured. It was thus possible to analyse the percentage time spent by lizards for various activities and to assess those structures of the habitat which were ecologically important to an egg laying lizard.

Adult females selected the ground for 21.9% of the daily activity, and 78.1% was spent on trees. Males spent 40.4% on the ground and 59.6% above ground (Mendes, 1976). Both males and females have a preferred activity site, usually a tree in their territory, on which they spend most of the day's activity. The males have a number of trees in their territories and therefore a number of activity sites. The preferred site of the female is a static one. The preferred activity site of both males and females were located between one and two metres above the ground on trees such as *Jacaranda*, *Cassia*, *Delonix* and *Markhamia* species which were planted in the urban and suburban areas of the town.

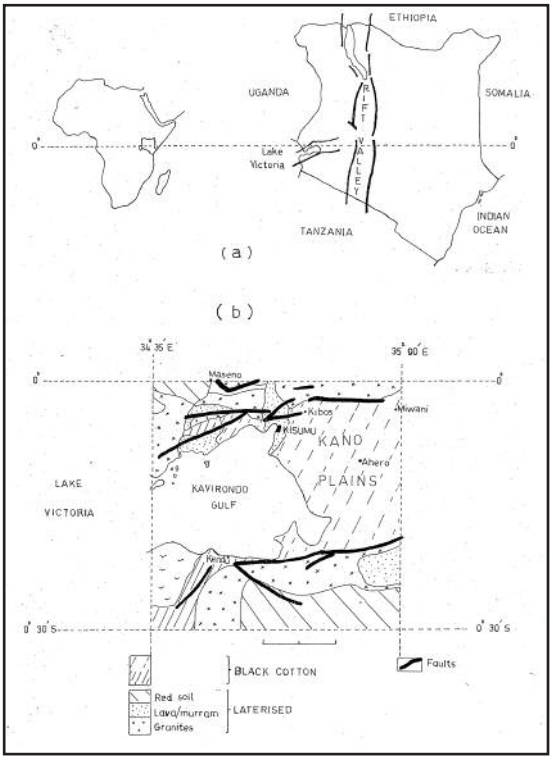


Figure 1. Map showing region of study (above) and geology and soil cover (below).

RESULTS AND DISCUSSION

Nest Site Selection

The relative frequency of nesting activity including pseudo nesting increases with time so that the peak of nest digging activity occurs near the end of the daily activity cycle (between 16:00 and 17:00 hr). After that, nest digging activity ceases as the maintenance activities of basking, resting and some feeding take priority in preparation for sleeping. Females are active for longer periods during the day (mean = 8.95 hours), emerging earlier and retreating later than the males. The nest digging activity reaches peaks in mid and late afternoon. This activity may or may not result in egg laying. Gravid females spend more time in site selection and they can postpone egg laying for a considerable length of time (several days). This can influence the daily pattern of diurnal activity as the females concentrate on nest digging (and trial digs) soon after mid-morning basking,

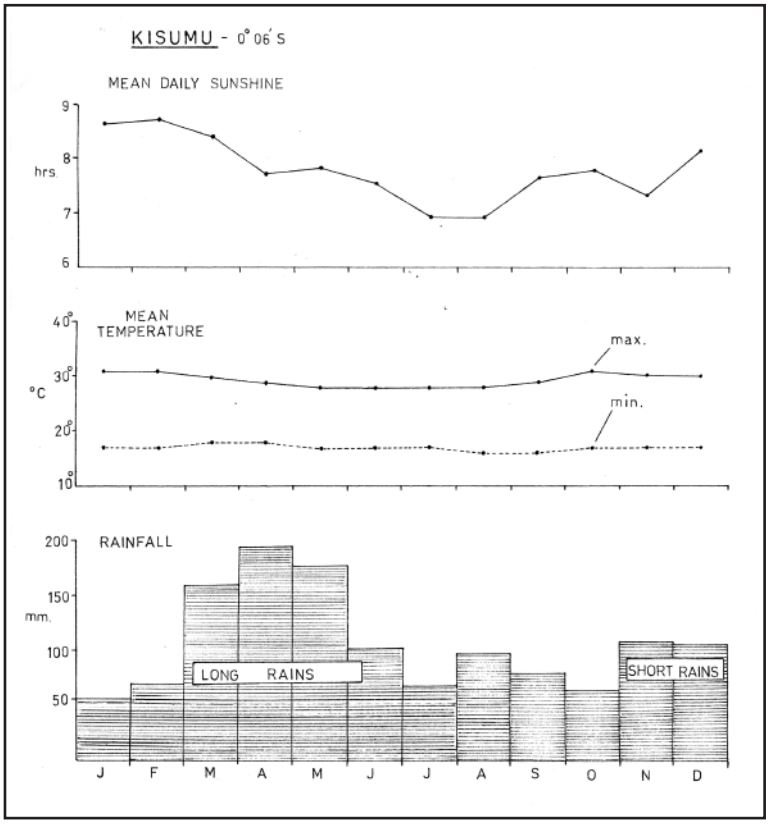


Figure 2. Climatological data for Kisumu.

Behaviour of the gravid female

The female lizard is entirely responsible for the excavation of the nest. As the time approaches for egg laying, the heavily pregnant female makes frequent excursions to the ground, generally moving short distances from the base of the tree, which has been used as an activity site. During these excursions, the attention of the female focuses on ground suitable as a nesting site. At first there may be a few desultory scratches made on the ground with one fore-leg only or with alternate fore-legs, resulting in the excavation of a very shallow depression, At this stage the female is easily distracted and interrupts her work to feed or move to a new nest site, or to her preferred activity site (usually a tree) one to two metres above the ground. If disturbed she will quickly climb higher. During any one session, the female keeps to a general type of site with similar characteristics, usually near cleared ground, and not too far from the preferred activity site. Later the same day (or sometimes in the next day or two), usually from 11:00 hr to 17:30 hr with a peak from 12:00 to 15:00 hr, nest digging activities become more marked. The female is found concentrating on nest digging on a particular site. When serious nest digging has begun the female is rarely distracted by food and returns unerringly to her partly excavated nest, and recommences digging after a quick look round. Many such depressions may be dug before the eggs are finally laid, at a depth of 8 cm and the nest covered. Pseudo- nests are always left uncovered and are the result of shallow depressions of varying depth left in the ground. Bellairs (1969), writing on the Bengal monitor, reports it as excavating several additional pits over or near the nest which may have the object of misleading the predator. Harris (1964) writing on *Agama agama*, expresses the view that 'after spending so much energy on digging,…….the hole may not be used at all'. With a view to throwing some light on this subject, an examination of pseudo-nests was made to find out the following:

a) whether the pseudo-nests dug were ' decoys' to detract attention from the actual nest sites, or

b) whether the sites were unsuitable in any way,

Pseudo-nests and case history notes

The nesting activities of 10 females are given in Table 1. It appears that most attempts at nest construction took place a short distance from the nearest cover, usually in bare soil, exposed to the sun from five or more hours a day. In fact the data obtained for pseudo-nests closely parallels the data for actual field nesting sites, suggesting that some other factor or factors may contribute to the female abandoning the hole or nest site. From the data in Table 1, it appears that in a number of cases

Nest Site Measurements (cm; mean±SD)				Nest Site Requirements (%)														
	Depth	Surface Diameter	Distance from nearest cover	Cover			Soil Moisture			Soil Surface			Sub-soil			Shade	Sun	
				Bare	*Low grass*	*High grass*	*Dry*	*Damp*	*Wet*	*Loose*	*Compact*	*Rocky*	*Loose*	*Compact*	*Rocky*		*Half day*	*Full day*
Final Nest (*n* = 10)	8.0±0.52	5.18±0.44	122.1±87.32	40.0	60.0	-	-	100.0	-	-	100.0	-	-	100.0	-	-	20	80
Pseudo-nests (*n* = 31)	2.3±1.99	3.2±1.31	142.2±23.14	61.2	38.7	-	-	100.0	-	6.4	93.5	-	12.9	41.9	45.2	19.3	54.8	25.8

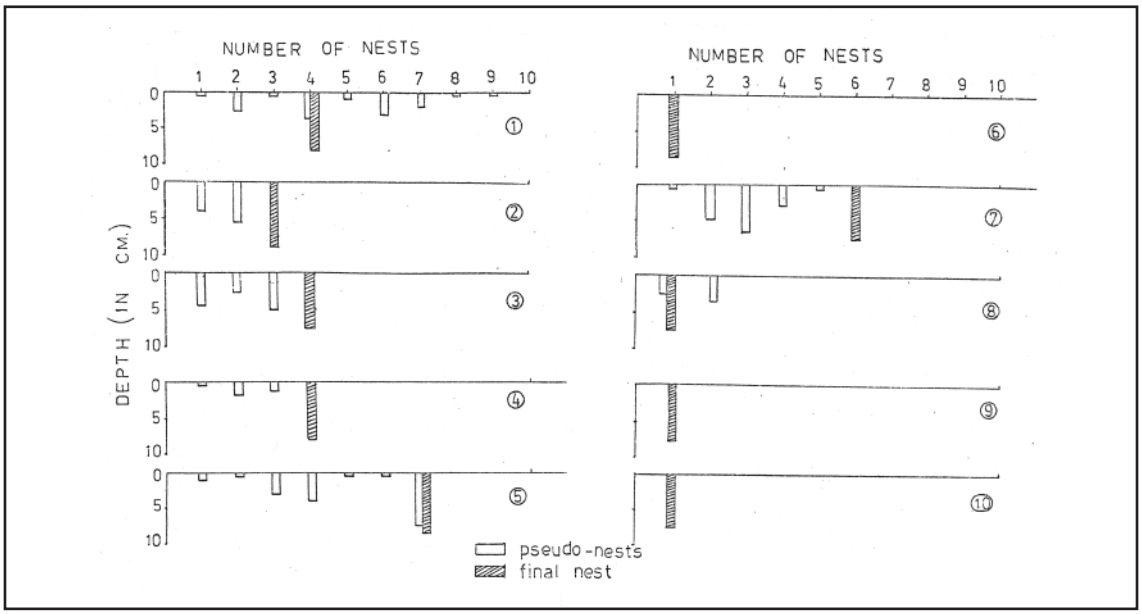
Table 1. Analysis of the nest site and site requirements of ten adult female *A. atricollis*.

underlying immovable stones or rock, hindered further digging and caused the female to move to another site, and start digging anew. This suggests that these pseudo-nests were just unworkable sites which were abandoned. Yet, on the other hand pseudo-nests were dug and abandoned, in soil that appeared to have all the characteristics of a suitable site. Harris (1964) suggests that the female may experience an 'inward drive' to start digging holes as the time for egg laying approaches, although she may not be ready to lay her eggs.

The following case history reports are observations on female lizards and throw some light on this issue:

Case History 5 (10th March 1971) – A heavily pregnant female was seen to begin digging at 10:30 hr and was kept under observation until 16:30 hr. During this time she dug 7 pseudo-nests. As they were dug their positions and order of digging were noted on a map of the area. Her nesting activities ceased at this time when the air temperature began to drop and the sky became overcast. It was very windy and finally started to rain. The reaction of the female was to move 2 metres away from the nest site and towards cover provided by a tree where she remained until the rain began to fall. She then disappeared from view. On 11th March 1971, the pseudo-nests were examined again at 07:00 hr. Hole 7 was found to be filled slightly with soil as the sides of the nest

Figure 3. Sequence of nest digging from start to final egg laying. Hatched lines indicate depth of nest and site of final egg laying. Encircled numbers (1–10) depict the case histories of 10 nests between 1970–1973, with depth of nest dug given on the vertical scale, and number of nesting attempts on the horizontal scale.



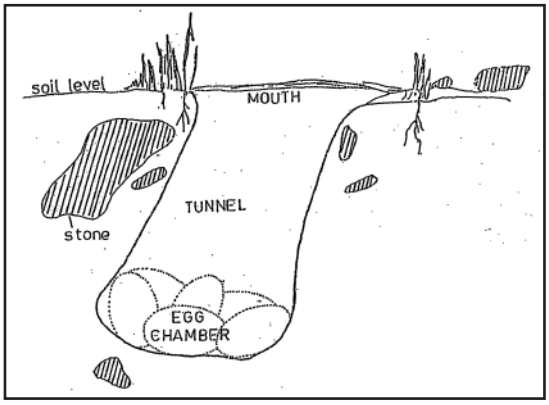


Figure 4. Nest structure and egg arrangement, showing single layer of eggs as positioned by the female.

collapsed inwards after the showers of the previous night. By 10:00 hr no eggs had been laid and my observations then ceased until about 12:30 hr when the nest site was examined again and hole 7 was found to be completely covered with soil and camouflaged. Seven eggs were found at the bottom of the nest at a depth of 8.5 cm. The 7th hole was obviously the correct depth for egg laying the previous day, and had the environmental conditions not drastically altered she would have undoubtedly laid her eggs between 16:00 and 18:00 hr on 10th March 1971. This implies a postponement of egg laying by 18–20 hours.

Table 2. Characteristics of nest sites.

Condition		Number of nests	
		Observed	Pseudo-nests
Soil Surface:	Loose / disturbed / cultivated	1	2
	Compact / undisturbed	25	29
	Hard / rocky	0	0
Sub-soil:	Loose	1	4
	Compact	25	13
	Hard / rocky	0	14
Soil moisture:	Dry	0	0
	Damp	25	31
	Wet / waterlogged	0	0
Sunshine:	Complete shade	0	6
	Sun – half day	13	8
	Sun – fill day	13	17
Cover:	Bare soil	11	19
	Scanty / low grass	15	12
	Moderate – high grass	0	0
Distance to nearest cover:	< 1 metre	19	13
	1 – 2 metres	6	10
	> 2 metres	1	8
Direction of nest entrance from nearest cover:	Facing away	20	-
	Facing towards	-	-
	Other	6	-

Case History 3 (9th August 1973) – On 9th August 1973 a nest hole was discovered in the garden in an area of scattered low grass and bare soil. No pseudo-nests were found and neither was the female seen. The nest was 7 cm deep and 5.5 cm wide. The nest was observed at 12:35 hr. At 15.00 hr the site was examined again and was found to be undisturbed. No other pseudo-nests were found in the area.

On 11th August, at 10:00 hr and again at 12:30 hr the female was observed at the site digging. She proved to be one of my marked lizards. She was extremely wary and retreated into the hedge 3.5 metres away, when she caught site of me. The nest was then 7.5 cm deep. At 15:00 hr the female returned to the nest site and was observed with binoculars until signs of egg laying were evident (see Egg Laying Behaviour, page 20), after which the female made no attempt to escape on closer approach. Data from field notes are given below:

15:22 hr. Nest digging complete. Female enters nest.

15:23 hr. Sinuous posterior body movements alternate with brief rest periods. The mouth open panting posture assumed.

15,30 hr. First egg laid.

15:37 hr. Sixth egg (final egg of clutch).

15:40 hr. Emerges from nest and surveys surroundings.

15:42 hr. Inspects the eggs and prods them.

15:45 hr. Soil pushed back into nest. Packing and camouflage of the nest begins. Uses the forelimbs and sometimes the hind limbs to push soil into the nest.

An estimated postponement of egg laying by 48 hours is indicated in this case and it suggests that females of this species are capable, under adverse environmental conditions of postponing egg laying for much longer. Observations on the digging activities of females in sequence from the start of nest digging (pseudo-nests) to actual egg laying is given in Figure 3.

On three occasions, pregnant females were seen to lay eggs in the first hole dug (Cases 6, 9, and 10 Figure 3). A search for pseudo-nests in the area was unsuccessful. It is possible that the females were more mature and experienced with a good knowledge of the habitat and substrata for egg

	Mean Depth (cm)	Distance from nearest cover (cm)	Cover (%)			Soil Condition (%)			Soil Moisture (%)			Shade	Sun	
			Bare	*Low grass*	*High grass*	*Loose / Cultivated*	*Compact*	*Rocky*	*Dry*	*Damp*	*Wet*	*Whole Day*	*Half day*	*Full day*
Observed Nests (*n* = 26)	7.96±0.40 (7.5-9.0)	97.73±67.66	42.3	57.6	-	3.8	96.1	-	-	100.0	-	-	50	50
Pseudo-nests (*n* = 31)	Varies	142.2	61.2	38.7	-	6.4	93.5	-	-	100.0	-	19.3	54.8	25.8

Table 3. Analysis of conditions for nest-site selection. Data recorded as mean ± SD (range).

laying. Perhaps the onset of nest digging and the urge to lay eggs could be associated with different hormonal levels.

Forty-five percent of the pseudo-nests had large stones and underlying rocks which could have hindered digging. Often, the final nest has been dug in the close vicinity of the pseudo-nests (see Fig.). Some females dig a number of pseudo-nests and abandon them. They later return to an earlier pseudo-nest to complete their nest digging and egg laying (see Cases 1 and 2).

Characteristics of nest sites

Nest digging usually begins just after a shower of rain when the soil is moist. Both pseudo-nests and observed nests were examined to determine those factors that might be important in nest site selection (Table 2). This is analysed further in Table 3 and discussed below.

Proximity to nearest cover

86.1 % of the nests examined were less than two metres away from the nearest cover – a hedge, trees, or tall grass, suggesting that either the females or hatchlings are vulnerable to predation. Although there are a number of known natural predators on the adults, predation is not high in this habitat due to the activities and presence of man. On the other hand, mortality rates of hatchlings are very high. It is suggested that proximity of nest sites to areas affording cover is to allow hatchlings to escape predation and possible overheating. The natural shyness of the female and her vulnerability while nest digging are other possible considerations.

Soil conditions

Since both pseudo-nests and the final nest site are constructed in the same general area, females appeared to be consistent in their choice of nest sites. Nintey percent of attempted pseudo-nests and final nests occurred in compact, undisturbed soil. Since nest digging activities commenced soon after the rains, the role of moisture as a factor in nest siting appears significant. Loose soil, while having excellent aeration, has insufficient moisture retention properties. Field observations

Table 4. Analysis of measurements taken of observed nest sites.

Number of observed nests	Depth (cm) mean±SD (range)	Width (cm) mean±SD (range)			% Orientation (relative to cover)		
		Mouth / Entrance	*Tunnel*	*Egg Chamber*	*Facing away*	*Facing towards*	*Other*
26	7.96±0.46 (7.5–9.0)	7.38±0.83 (6.5–9.0)	5.0±0.40 (4.5–5.8)	6.0±0.33 (5.0–6.0)	76.9	-	23.1

Figure 5. A female pauses during the course of nest-digging to survey her surroundings.

Figure 6. Typical nest-digging posture.

Figure 7. Egg-laying posture of *A. atricollis*. Two eggs are visible in the nest.

Figure 8. Panting is shown by female during the course of egg-laying.

Figure 9. Female replacing soil in the nest after egg-laying (early stage). Note packing posture.

Figure 10. Female camouflages the completed nest.

Mature Female (mean ± SD)		Eggs when laid (mean ± SD)		Embrionic Stage[1]	Clutch Size (mean)
S-V length (mm)	Weight (g)	Length (cm)	Weight (g)	27 (mean)	7
90-99[2,3] to 120-129[3]	29.30±3.0 to 50.98±7.64	2.00±0.05 *(n=78)*	1.82±0.21 *(n=78)*	24-30 (range)	

Table 5. Aspects of egg laying in *A. atricollis* ([1] Dufaure & Hubert, 1961, and [2]Reaney & Whiting, 2002; [3]Mendes, pers. data). S-V length: 90–99 = minimum size of ovigerous females; 100–119 = size at which females were most prolific in terms of egg production and clutch size; 120–129 = very large females showing a slight decline in clutch size.

on the care and packing of the soil by the female into the nest, further stresses the importance of moisture retention by compact soils. Eggs that are in water logged soil quickly develop fungi on them. Fifty percent of the nests were dug in bare soil, the rest between patches of low grass cover. All nests were sited so that they had 5 hours or more of sunshine.

Nest digging (Figures 5 and 6)

Nest construction is performed exclusively by the female. The fore legs are used in turn for excavating a hole, and in pushing away earth which collects at the rim of the hole. The hind limbs are also used in pushing soil away. During the final stages of nest digging (Figure 6) the female's head is well within the nest and the action of the forelimbs is one of scratching and also scooping of the soil out of the nest. During this activity the female frequently stops and surveys the surrounding area. When a sufficient depth has been reached the female enters sideways into the nest. A suitable nest depth appears to be one where her forelimbs and head just extend above the rim of the nest with the hind limbs just touching the bottom (Figure 7).

A pregnant female is extremely wary when on the ground. From the onset of nest digging until just prior to egg laying, the female will retreat at the slightest signs of movement or disturbance. It is only when she enters the nest for the purpose of egg laying that escape tendencies are replaced by guarding and aggressive behaviour.

A vertical section of a typical nest (Figure 4) shows it as a slightly inclined tunnel, approximately 8 cm in depth, with the entrance to the nest wider than the rest of the tunnel and almost circular measuring 6.5–9 cm in diameter. The base of the nest or egg chamber is slightly rounded, being only slightly larger than the diameter of the tunnel. Table 4 shows measurements taken at 26 observed nest sites.

The nest is orientated in such a way that its mouth faces away from the direction of nearest cover (Table 4). While digging the female invariably faces the direction of nearest cover. Her digging activities result in one side of the rim of the nest having a more gradual slope than the rest. Consequently, measurements taken at the rim varied.

During egg laying, the female enters the nest, and in a head up position, peers over the rim of the nest, her fore limbs gripping the gently sloping sides. At this time she is facing away from the direction of cover.

This behaviour of the female indicates that during the actual digging of the nest the safety of the female herself is of prime importance, and hence she faces the direction of cover to enable her to make a hasty retreat. During the actual laying of the eggs, the defence of the nest is of prime concern. This defensive attitude is so strong that only rarely will she leave the nest even when approached to within a metre by the observer. This behaviour is totally different from the normally shy and wary behaviour of these animals.

Peak egg laying (Figures 7 and 8)

The correlation of breeding activity in lizards and rainfall has been suggested by a number of workers. Harris (1964), Daniel (1960), Inger & Greenberg (1966) showed that constant egg production was maintained by lizards in a relatively unvaried equatorial climate. At Kisumu there is usually some rain in every month, though this pattern can vary from year to year. During

1972 more then 50 mm of rain fell in eleven months of the year. In 1973 there were only seven months when the rainfall was 50 mm or more. Females with eggs in the oviduct are easily discernible. In the field observations on known territorial females were made to ascertain the times of egg laying. In all cases, nest digging and subsequent egg laying occurred within days after the first rains, following a drier period and also with the cessation of rain following a rainy period. Nineteen egg laying instances were observed in the years 1972–73. In the majority of cases, actual egg laying coincided with the end of the dry season and onset of the rains, or just after the end of the rains

The timing of egg laying in *Agama atricollis* varies from year to year depending on annual variations in rainfall and suggests that the species while potentially capable of egg production all the year is responding to local climatic conditions.

The presence of oviducal eggs only indicates a readiness to lay but the actual egg laying may be postponed until suitable environmental conditions prevail. While the mechanism by which changes in the environment are transmitted to reproductive organs is incompletely understood other evidence supports the view that egg laying is moisture-dependent. Egg laying therefore occurs at the onset or end of the rains when the moisture content of the soil is sufficient to allow for nest digging and egg development.

Development stage at egg laying

In order to find out at what stage of development eggs were laid, at least one egg was opened from a newly laid clutch. An entire clutch was also opened to check the stage of development and note differences within a clutch. In every case embryological development had started before the egg was laid. At deposition the embryo was at a slightly advanced stage corresponding to stage 27 of the table of development as defined and illustrated by Defaure & Hubert (1961). In any given clutch all the embryos were in a similar stage of development. However, between clutches the stages of development at egg laying ranged from stage 24 to stage 30, providing further evidence concerning postponement of egg laying or enhancing the case for egg retention.

Egg laying behaviour (Figures 7 and 8)

Egg laying commences after the female has entered the nest .The head juts out of the nest, and the forelimbs are used to grip the rim of the nest. This is the position for egg laying to commence. During egg laying, the mouth opens, and panting alternates with frequent swallowing movements. The tail may be raised or placed to one side. Sinuous movements of the posterior part of the body occur as each egg is laid. The following observations record egg laying in a marked female initially on the 9th August 1973 and continued on 11th August 1973 (See Case 3).

Packing and camouflage of the nest (Figures 9 and 10)

Once the eggs have been laid, the female arranges and pack them in the nest using her snout. She then starts to replace the soil using the forelimbs and sometimes the hind limbs to push soil into the nest.

Egg arrangement

Eggs are packed tightly in a single layer in the nest. Generally the eggs lie with their long axis horizontally placed on the floor of the egg chamber-only occasionally is the long axis of the egg in a vertical or obliquely placed position. In no cases have I recorded eggs being one on top of the other or in layers. This single layer arrangement would thus give all the hatchlings equal chances of scrambling out of the nest, which would otherwise be difficult if other eggs above them had not yet hatched. The pliable nature of the egg allows the close fit and packing of the eggs against one another and the walls of the chamber.

At frequent intervals during this packing process, the female puts her head and forelimbs into the nest and proceeds to pack the soil on top of the eggs using her snout and lower jaw. At the same time a rapid packing movement using the forelimbs occurs (Figure 11) which involves scooping soil towards the snout to facilitate packing. Rapid forelimb movements (drumming) compact soil into the nest. The entire body may whirl in a clockwise and anticlockwise movement during this packing process. Packing movements alternate with brief periods of rest and surveying of the surroundings. The female urge to protect her nest is very strong during the filling and packing stages. On the approach of another lizard, the

mouth opens and the gular pouch is extended, a characteristic of aggression. If the female is removed and displaced a short distance from her nest, she will on being released immediately returns to her nest site and continues to pack and cover the nest. As the nest is filled the urge to protect the nest wanes and gradually moves further away from the nest site, still scratching away at soil until she returns to her preferred activity site. On completion of nest packing, the female displays no further interest in the nest site.

The Kisumu population of *Agama atricollis* has a mean clutch size of seven. Fitzsimons (1943) in South Africa records a clutch size of 8–14, while Robertson *et al*. (1965) at Lake Rukwa (Tanzania) where the annual climate is characterised by one dry and one wet season, obtained a mean of about eleven eggs per clutch. This wide range of clutch sizes emphasises further the potential reproductive variability of *Agama atricollis* and no doubt accounts for its wide geographic distribution and success. This also supports Tinkle's (1967) contention that small clutch sizes indicate that a species reproduces more often, and that a large clutch size may be indicative of a drop in the number of clutches.

The eggs of *Agama atricollis* when first laid are creamy white in colour with a pliable and parchment-like shell. The shape of the egg is ovoid with rounded ends. The largest egg recorded from a clutch measured 2 cm long, and 1.2 cm wide when first laid. The mean measurement of eggs from observed nest sites were as follows: length 2.00 ± 0.05 cm. Further aspects of egg-laying are indicated in Table 5.

Gordon (1956) suggested that captive lizards could be induced to oviposit by spraying them with water. Stamp (1976) reported on an experiment that was performed, in which small patches of ground 5m x 5m each, were watered with 5 litres of water and how several lizards (*Anolis aeneus*) came to the watered site and laid eggs. Females in non-watered areas continued to dig holes, but did not lay eggs. Stamp (1976) also noticed that female inserted the tip of the snout into a nest hole site and this occurred during hole digging.

Females appear to sense the moisture content of soil and choose to lay in moist areas. It is possible

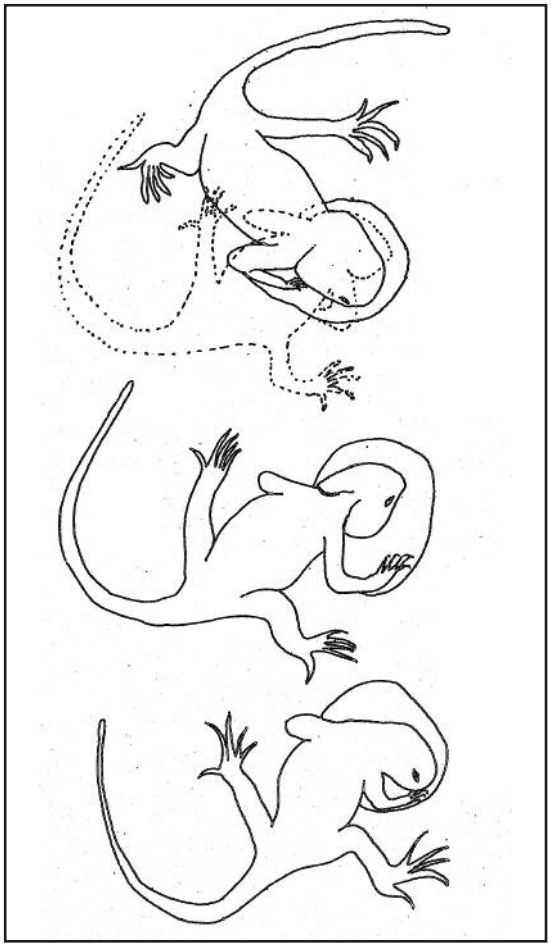


Figure 11. Nest-packing movements of *A. atricollis*.

that during nest digging, periodic probing of the soil in the nest or pseudo-nest allows the female to gauge soil moisture content (Stamp, 1976).

Workers involved in the pet trade are aware that terrarium lizards could be induced to oviposit by spraying the lizards with water (Manthey & Schuster, 1996). It is possible that the pseudo–nests encountered in the field were unsuccessful attempts at finding the right amount of moisture for their eggs to develop. Laying eggs in dry soil led to problems of desiccation. According to Stamp (1976), it is rainfall which induces digging and sensing moisture by snout probing which induces egg laying.

Hatching of agamid eggs in the laboratory in soils of different percentage saturation was attempted after the method of Lewis & Taylor

(1967). In soils of 0.5% saturation, all the eggs desiccated within a few days. Excess moisture resulted in the spoilage of the eggs. Hatching success ocurred in soils with percentage saturation of 1–3% saturation (Mendes, pers. obs.).

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