FEEDING, SOCIAL BEHAVIOUR AND TEMPERATURE PREFERENCES IN *AGAMA ATRA* DAUDIN (REPTILIA, AGAMIDAE).

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ABSTRACT

Agama atra is mainly insectivorous, ants being the main food of juveniles, and larger insects that of adults. The lizards are territorial and hierarchical and perform elaborate aggressive and courtship displays on prominent rocks. In the field, routine activities commence at an air temperature of about 19° C and reach a peak at the hottest time of the day. Lizards acclimated at 26,5° C in a vivarium showed a modal preference for temperatures from 32° to 34,9° C; those at 39,4° C for temperatures from 35° to 43,9° C. Pre-chilled and pre-warmed lizards increased and reduced body temperatures respectively by behavioural means. Submissive and protective behaviour affected temperature preferenda. *A. atra* is a heliothermic ectotherm capable of selecting optimal temperature zones and modifying body temperature by basking and adopting different postures and orientations in relation to the heat source.

INTRODUCTION

Investigations into the natural history of southern African lizards have lagged far behind studies on their taxonomy and distribution. Brief field notes were given by FitzSimons (1943) and more recent work includes that of Broadley (1967) on lacertids; Brain (1961), Spence (1966), Burrage (1973) and Broadley & Blake (1974) on chameleons; and Haacke (1974, 1975) on geckos. Mark/recapture studies are reported by Broadley (1974), and research on temperature tolerances by Stebbins (1961) and Brain (1962).

Agama atra Daudin 1802, the South African rock agama, is a common diurnal lizard found on rocky hills and mountain slopes in South Africa, Botswana and Lesotho (FitzSimons 1943). FitzSimons provided field notes on *A. atra*, and Burrage (1974) studied spatial and social organization in this species as well as in *Cordylus cordylus cordylus*. Investigations into closely related species include those of Cowles (1956) on *A. atricollis* in South Africa and Harris (1964) on *A. agama* in West Africa.

The present note describes field and laboratory observations performed in 1969 on feeding, social behaviour and temperature preferences of *A. atra* on Gunfire Hill, Grahamstown, in the eastern Cape Province. The study had two aims: (*a*) to describe aspects of the ecology of *A. atra* in a relatively cool part of its range, and (*b*) to determine the requirements of *A. atra* in terms of food, social grouping and temperature preferences to provide information on their housing requirements for later experiments in a semi-natural environment.

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METHODS

Lizards were collected in the field by shooting with rubber bands (Brain 1959), and marked with paint for identification in the field and laboratory. Laboratory observations were made in an indoor vivarium 2 × 1,5 m with hardboard walls 1 m high. The floor consisted of a sheet of softboard covered with sand and rocks from the habitat. The vivarium was housed in a constant environment room, usually at 32±1°C unless otherwise indicated. Light conditions were maintained at 12 hours dark (18h00 to 06h00) and 12 hours light. A screen was constructed across one corner and side of the vivarium, and observations were made through a number of slits without alerting the lizards. The noise level in the room was high but constant. Further methods are mentioned under appropriate headings in the text.

RESULTS AND DISCUSSION

FEEDING

Field observations indicated that feeding takes place on clear warm days when air temperatures exceed 19°–20°C (N = 32 days). Fifty-three direct observations, and the examination of stomach contents and faecal pellets (Table 1) revealed that ants (*Cromatogaster peringueyi* and *Pheidole megacephala*) formed the bulk of the diet. Small grasshoppers, honeybees (*Apis mellifera*) and small beetles were also taken. The importance of relatively large items in the diet should not be underestimated. *C. peringueyi* and *P. megacephala* had a mean mass 30 to 40 times less than that of the grasshoppers and beetles taken. The relatively small proportion of non-ant food is thus likely to contribute significantly to the diet of *A. atra*. FitzSimons (1943) reports that *A. atra* feeds largely on ants (Poneridae), together with grasshoppers, beetles, cockroaches, crickets, fossorial wasps, millipedes, spiders and leaves, and Burrage (1974) that intertidal arthropods may also be taken. Harris (1964) found that 95,5 percent of the food of *A. agama* consisted of ants, and that only three other orders of insects contributed significantly to the diet (*i.e.* Coleoptera, Hemiptera and Orthoptera). Ants also constituted 96,1 percent of the food of *A. atricollis* (Cott 1934).

The lizards were offered fourteen different species of insects in the vivarium, including Coleoptera (Carabidae, Tenebrionidae, Elateridae), Hymenoptera (ants and bees), Hemiptera (Reduviidae, Pentatomidae), Isoptera (*Calotermes* spp. and *Trinervitermes* spp.) and Lepidoptera (Noctuidae, Pieridae, Nymphalidae). All the offered items except *Trinervitermes* soldiers were taken, but small agamids (snout-vent length less than 60 mm) showed a marked preference for smaller prey (ants, termite workers and small beetles) and larger agamids for large Coleoptera, Hemiptera and Lepidoptera. *Tenebrio molitor* larvae (mealworms) as well as cabbage leaves were readily eaten by large agamids. Small agamids captured prey using the sticky tongue, but in larger lizards the prey was snatched up in the jaws. The lizards locate their prey mainly by sight, and eat only moving prey. This was demonstrated in a simple experiment (repeated 15 times) on a captive male lizard. Six dead *Trinervitermes* workers were placed on a glass plate, three of which were glued in place; the lizard showed no interest. When the three unattached termites were made to move by directing a jet of air on them, the

TABLE 1

The food of *A. atra* on Gunfire Hill, Grahamstown.

(*a*) Examination of stomachs

Lizard age-groups	*Stomach contents*
1. Juvenile (snout-vent length less than 60 mm)	All ants.
2. Juvenile	All ants.
3. Juvenile	All ants.
4. Juvenile	All ants.
5. Adult	Mostly ants, 4 acridid hind femora, elytra of 3 beetles.
6. Adult	Mostly ants, numerous beetles.
7. Adult	Mostly ants, few beetles, one acridid.

b) Examination of faecal pellets

Lizard age-group	*Faecal pellet contents*
8. Adult	1 acridid hind femur, remains of *Apis mellifera*, several small beetles.
9. Adult	1 coccinellid elytron, remains of 3 *A. mellifera.*

lizard immediately snapped them up, but left the three fixed termites.

A marked preference for *Trinervitermes* spp. workers as opposed to soldiers was noted. The soldiers are of the nasute type and eject a repellent secretion from the frontal gland. *A. atra* in captivity could not be induced to eat the soldiers at all, whereas live workers were readily taken.

A. atra kept in vivaria for subsequent studies was fed on termite workers and *T. molitor* larvae. Both prey species were easy to culture in the laboratory, and catered adequately for the needs of small and large agamids. The lizards remained healthy on this diet judging by their high level of activity and maintenance of mass. Other workers have also found that this diet is sufficient for lizards in captivity (e.g. Dawson 1960, in the skink *Eumeces obsoletus*).

SOCIAL BEHAVIOUR

Social structure of the community

Agamids, in common with many other species of lizards, are social animals – they form pair bonds, establish and defend territories, maintain a social hierarchy and regularly communicate to one another their relative status by means of aggressive displays. An integral part of agamid social behaviour is territoriality, therefore territory size and establishment will be discussed first. Other aspects of social behaviour will then be commented upon.

Territoriality

Studies of territoriality in lizards are numerous, and in agamids include those of Lamborn

(1913), Harris (1964) and Burrage (1974). There is considerable variation in the size and structure of agamid territories but three important structural components are usually found: (*a*) a suitable display post for the dominant male, (*b*) a roosting place and (*c*) conveniently situated refuges from predators. The display post is the focal point of any territory and territorial group. In every territory-owning individual the readiness to fight is greatest at the display post and least at the territorial boundary. Lorenz (1968) noted that, as the distance from the perch increases, the threshold for fight behaviour increases. The boundary of the territory will be found where the tendency to fight and the tendency to flee back to the display post are roughly equal.

In *A. atra*, each new generation of males has difficulty in establishing territories. Most take possession of small territories in suboptimal parts of the biotope, then gradually encroach on the territories of larger males, and eventually may depose them. Competition for territories is highest when population density reaches a peak. Manning (1967) has likened territories to elastic discs – the more they are compressed, the more they resist further compression.

In the agamid colony on Gunfire Hill, 13 display posts were identified, of which four were chosen for further study. The boundaries of the territories were determined by observing the range of movements of the dominant males. A minimum of 20 points was used for constructing each territorial boundary.

Two display posts were on high points of a long, low roughly-assembled stone wall. The territory of the first male stretched approximately 1,5 m back and 3 m forward of the wall. The other territory was larger, having a radius of 3 m around the display post. Crevices in the wall served as refuge and roosting places. Vegetation in the area consisted of grass, scattered exotic pines, numerous sclerophorous plants, and succulents such as *Crassula*. Large quartzite boulders and pine logs were scattered over the area.

The third display post, the highest point on a large pine log, overlooked a territory about 4 m in radius in the hollow of a small quarry. The fourth display post, on the highest point of a 1 × 1,5 m boulder on a steep rocky slope, dominated a territory stretching 0,75 m around the rock. Two other territories were established on similar boulders within 3 m of this territory. Lizards from the four territories served as observation groups in the field; lizards for experiments were obtained from other groups.

The areas of the four territories are compared with areas obtained by Burrage (1974) for *A. atra* and Harris (1964) for *A. agama* in Table 2. The relatively small size of *A. atra* territories on Gunfire Hill may be due to the high population density of adults, which varied between 160 and 210 lizards per hectare in the study area. This figure is higher than that given by Burrage (1974) for coastal cliffs (125/hectare) and inland rock outcrops (51/hectare). Burrage states that adult population density in *A. atra* varies inversely with territory size.

Dominant males defended and remained within their territories throughout the year, but subdominant males, females and especially juveniles crossed territorial boundaries. Home ranges are not found in the case of dominant males as the whole occupied area is defended. On one occasion a territorial male was removed from his territory, whereupon a subdominant male took over the display post. The boundaries of the new territory were different under the new incumbent, whose territory was initially smaller but eventually equalled the previous territory in size but not in shape. Male territories are always largest, and may contain smaller,

TABLE 2

Territory size in *Agama atra* and *A. agama*.

A. atra (present study) *Dominant ♂♂ only*	*A. atra* (*Burrage* 1974)	*A. agama* (*Harris* 1964)
Territory 1 – 12 m^2	Coastal cliffs	Usually 42–56 m^2.
Territory 2 – 28 m^2	average 92,5 m^2 ♂♂ 56,0 m^2 ♀♀	Under extreme territorial pressure, 14–21 m^2
Territory 3 – 50 m^2	Inland rocky outcrops	
Territory 4 – 17 m^2	average 120 m^2 ♂♂ 77 m^2 ♀♀	
Average 26 m^2	♂ 106,3 m^2 ♀ 66,5 m^2	49 m^2 (normal) 17,5 m^2 (extreme)

less well-defined female territories.

Territorial display by dominant males and females.

Dominant male (and occasionally female) *A. atra* perform aggressive displays in defence of their territories. As with most lizard displays, they may be either assertive, *i.e.* a low intensity warning performance, or challenging, *i.e.* a high intensity aggressive performance (Carpenter 1967). The display is usually initiated by the display of an adjacent dominant male from its display post (assertive response) or by the approach of an adjacent male towards the common territorial boundary (challenge response). The defending male displays by turning broadside to the intruder, swishing his tail jerkily a few times, and expanding the dewlap and nuchal crest. The dewlap, as well as the transverse fold of the neck, upper legs, throat and chest, assume an ultramarine blue colour, and the sides of the body turn purplish-red or pink. The bright-red interior of the mouth is also displayed, and bobbing movements of the head and forebody are performed. The intruding lizard also displays an ultramarine gular fold and raised nuchal crest, but head-bobbing is usually hesitant if the lizard is far from its display post. If the intruder is not frightened off by the initial threatening display, the defender runs rapidly towards the intruder, stops at a distance of 80–100 cm and assumes a broadside, stiff-legged challenge posture. The intruder usually flees at this stage, and is chased across the territorial boundary. The winning male then returns to a suitable perch or the focal display post and bobs his forequarters for a few minutes. Occasionally the intruder stands his ground during the challenge display and a brief combat ensues, with the lizards standing broadside to one another. Actual combat between dominant males was only witnessed on three occasions, each lasting less than five seconds. Tail-slapping was the only form of bodily contact observed; no biting took place.

If one lizard is larger than the other, fear will be aroused to a lesser extent in the larger one, as he is faced with a less frightening display, and he will tend to attack. The smaller lizard, in which inhibition of aggression and stimulation to take flight are more marked, will tend to flee. Thus, merely by means of a display, the lizards communicate to each other their relative status. The development of more and more impressive display colours, dewlaps, etc. may result in a decrease of intra-specific fighting, as the subdominant lizard is more likely to flee soon after the conflict begins. Natural selection has favoured the development of a symbolic display which achieves the functions of fighting, without reducing the ability to fight, but does not result in harm to conspecifics (Lorenz 1968).

Non-territorial displays

Besides the threatening and challenging head and upper-body bob described above, a peculiar nodding action of the head was also seen in *A. atra* colonies in the field. Almost simultaneously a group of lizards on basking perches will commence to nod the head in a slow, deliberate manner. The body remains stationary. After 5–15 seconds the behaviour ceases. This action has been described as "head nod" (Harris 1964) and is also recorded in *A. agama* and other agamids. Harris suggests that the head nod has some significance in the spatial relationships among individuals of territorial species by indicating their position relative to other lizards of the same group.

Minor aggressive skirmishes for suitable basking areas occasionally take place between juveniles and between subdominant adult females. These brief conflicts involve head-butting, light lumbar- and neck-biting and chasing, but no colour changes occur.

Courtship and mating

Courtship displays were often witnessed in the field and laboratory, usually between a dominant male and the adult female with which he shared the focal display post. During the hottest part of the day, the male would suddenly perform a head bob similar to that in the threat display, and then run rapidly towards the female. The female usually responded by adopting a submissive posture by lowering the head and arching her back. When the male approached to within a short distance, the female darted to one side, postured again broadside to the male and held her tail vertically. When approached again the female presented her posterior, then moved away in stiff-legged jumps to one side. When attempting to catch the female, the male occasionally executed a light lumbar bite. Mating was not observed.

Group size

Groups of lizards were collected from four different territories. In all cases the territories were centred around one boulder which, when rolled over, revealed the lizard group. The composition of the four groups is given in Table 3.

Each group consisted, on average, of one large male (probably dominant), one other male, two to three females, and about five juveniles, totalling nine individuals. Territories 1 to 4 (Table 2) each contained one dominant male, one or more other permanent adult males (although itinerant males were occasionally present), two to five adult females, and three to 12 juveniles; an average group size of 10–12 individuals.

Hierarchy in social groups

The status of a lizard appears to be related to the height at which it sits – dominant

TABLE 3

Composition of four natural territorial groups of *A. atra.*

	Adults			*Juveniles*	*Total*
Group	*Large ♂♂*	*Other ♂♂*	*Females*		
1	1	0	2	8	11
2	1	0	3	1	5
3	1	1	2	6	10
4	1	2	3	4	10
Average	1	0,75	2,5	4,75	9

lizards were observed on the highest rocks, and subdominant lizards usually occupied lower perches. Thus to determine the relationships between individuals, a natural group of lizards was allowed access to a pile of rocks. Details of the lizards used in these and other experiments are given in Table 4.

TABLE 4

Details of *A. atra* used in social hierarchy and temperature preference experiments.

Name	*Snout-vent length cm*	*Sex*
A	9,2	F
B	7,5	F
C	6,0	F
D	12,3	M
E	12,8	M
F	9,8	M
G	4,4	M
H	9,3	F
I	8,5	F
J	5,4	F
K	8,9	M
L	8,2	F

Burrage (1973, 1974) noted that antagonistic behaviour in lizards may increase or decrease in captivity, and Hunsaker & Burrage (1969) found a shift from territories to social hierarchy, with a development of despotism, as a result of population pressure and reduction of the available area. Social hierarchies have also been found in wild populations of lizards with high densities *e.g.* by Evans (1951) and Harris (1964). The present study population showed approximately the same degree of territorial and hierarchical behaviour in field and laboratory, probably because the field population was naturally stressed.

(i) *Establisment of status in adult females.* Three females were introduced into the empty vivarium in which five equal-sized rocks had been arranged as shown in Figure 1A. Notes were made at irregular intervals throughout the diurnal cycle on the position of each lizard on the rocks to determine whether any rock preferences were established, allowing at least 10 minutes between individual observations; 321 spot observations were made over nine days. As shown in Table 5, a marked preference for Rocks 1 and 5 in lizard A, and for Rock 1 in lizard B was found. Lizard C has a less-marked preference for Rocks 1 and 2. The lizards were often seen to lie on top of one another and appeared to have no individual distance – the distance in an aggressive flocking species to which one individual can approach another usually of the same sex (Lorenz 1968: 25). No conflict behaviour was noted during the experiment.

TABLE 5

Preference of lizards A, B and C for rocks arranged as in Figure 1A.

Lizard name	*Rock number*				
	1	2	3	4	5
A	116	26	26	22	131
B	150	55	35	26	55
C	103	96	55	19	48
Total %	38	18	12	7	25

(ii) *Establishment of status in adult males.* Two adult males (D & E, Table 4) were placed in the vivarium in which a pile of 10 rocks had been arranged as shown in Figure 1B. The position of each lizard on the rock-pile was noted at irregular intervals; 136 observations were made over three days (Table 6).

No conflict displays were seen but by the end of the second day lizard D, though slightly smaller, occupied a consistently higher position on the rock-pile than lizard E. When introduced into the vivarium, D was the first to reach Rock 1, the best display post. This may have been critical as Harris (1964) has noted that a lizard which succeeds in displaying from the major display post of another territory usually succeeds in gaining possession of that territory.

Both adult male and female *A. atra* showed preferences for a particular rock. In the

TABLE 6

Preference of lizards D and E for rocks arranged as in Figure 1B.

Lizard	*Snout-vent length*	*Rock number* 1	2	3	4	5	6	7	8	9	10	*On ground*
D	12,3 cm	30	0	0	0	0	0	0	0	0	0	5
E	12,8 cm	0	0	2	0	0	18	0	0	0	7	9

male 'possession' of a rock restricted occupation of that rock by another male. These observations were confirmed in the field.

(iii) *Establishment of status in a natural group.* A natural group of six *A. atra* (D, F, G, H, J, K: Table 4) was introduced onto a pile of 10 rocks as illustrated in Figure 1B. Records of the position of each lizard were made at irregular intervals during the day and night; 612 spot observations were made over eight days.

Time-lapse photographs were also taken using an 8 mm movie camera with an electronic flash unit. The rock-pile was photographed at one frame per 30 seconds between 23h00 and 08h00, to cover the time during which direct observations were not made. The camera was activated using a signal marker activating a solenoid lever. No abnormal behaviour resulting from the flash was observed. The photographs showed that

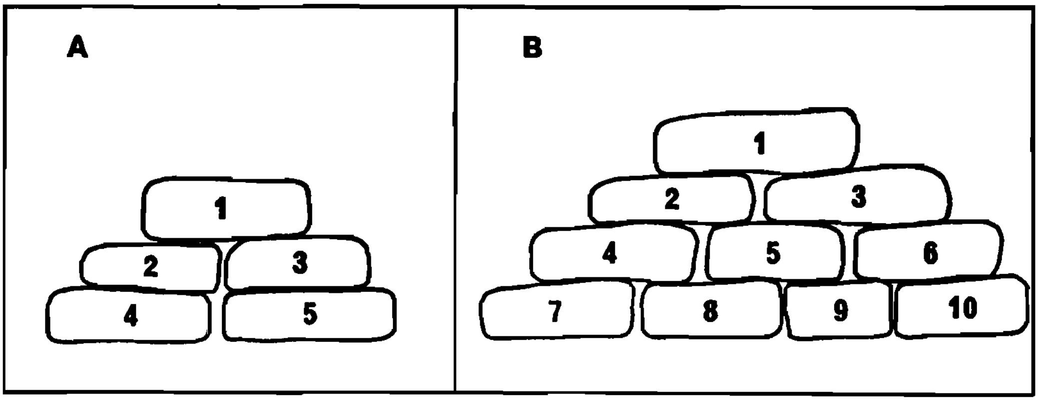

FIGURE 1

Rock-piles used for experiments on social hierarchy in *A. atra.*

hardly any activity took place at night, but otherwise confirmed results obtained from spot observations (Table 7).

TABLE 7

Preference of lizards D, F, G, H, J, K for Rocks 1 and 2 in Figure 1B.

Lizard	*Sex*	*Rock* 1	*Rock* 2
D	M	48	0
F	M	12	0
G	M	9	0
H	F	37	4
J	F	8	37
K	F	0	0

These results suggest the following hierarchical arrangement of the group in the vivarium:
Rock 1: dominant male and female (D and H)
Rock 2: subdominant female (J)
Lower rocks: subdominant male (F), submissive juveniles (G and K).

The largest male and female lizards assumed the dominant positions in the group, and the dominant male only allowed the dominant female onto Rock 1. All observations of other lizards on Rock 1 were made when the dominant lizard had temporarily left it.

Discussion on social behaviour

Aggression, *i.e.* fighting or token fighting between individuals of the same species, is a common behaviour pattern in lizards. Lorenz (1968) emphasized the way in which aggression tends to spread individuals in an animal population as evenly as possible over the available habitat. The danger of a population settling in only a limited part of its range is obviated if mutual repulsion acts on individuals of the same species. This will bring about a regular spacing out so that available food is used to the full. The rapid spread of disease and ease of predation, both consequences of overcrowding, are also avoided. However, the most important function of aggression is probably sexual selection, which involves selection of the healthiest and strongest animals for reproduction, and is brought about largely by aggressive encounters between rival males. A powerful lizard will not only be more likely to establish and defend a suitable territory, but will also, by virtue of owning a territory, have more chance of forming a mating pair and producing offspring. Harris (1964) found in *A. agama* that the main function of a territory is to provide a mate; this conclusion probably holds for *A. atra* as well. Territories would then have the effect of enhancing the chances of reproduction as lizards living in close contact would be more likely to copulate than individuals living apart, especially if the female has a short period of oestrus.

Challenge and courtship displays are thought to have evolved from the behaviour patterns of defensive fighting (Tinbergen 1965; Lorenz 1968). Two lizards meeting at the boundary of their territories will have conflicting motivations. Aggression will be stimulated by the presence of the other individual but inhibited if the other agamid is of the same or larger size (perhaps from experience of previous conflicts) and by the fact that the defender is away from his modal station. Thus tendencies to attack and escape may be aroused simultaneously, and it is reasonable to assume that a 'compromise' behaviour pattern will be performed (Manning 1967). Opened mouths, expanded dewlaps and flashed colours are typical of attack behaviour. The lateral position may be interpreted as part of an escape reaction (Lorenz 1968, in cichlids, which also have a lateral display). Manning (1967) has suggested that the inflation of air-sacs (*e.g.* dewlaps) is derived from the deeper breathing associated with taking flight. It seems as if those elements have been kept which present to the adversary the greatest display area and most intimidating postures, movements and colours.

Besides minimizing damage to conspecifics, ritualized threat displays in overt, diurnal lizards may also reduce the risk of predation (Tinbergen 1965). During combat two lizards with jaws locked would be easy prey to a predatory bird. A long period of copulation has apparently also been selected against (Bertin 1967).

Several workers have noted the similarity between courting and territorial challenge displays in lizards (Schmidt & Inger 1957; Harris 1964). Courtship displays may have been derived from aggressive displays performed by females during the breeding season. Aggression by the female would release an attack response in the male, who would, however, turn aside at the last moment when he sensed the female smell (Tinbergen 1965). The aggressive display of the male would arouse the female as well as bring about her submission. Their close proximity, and the natural arousal as well as the submissive posture of the female would greatly enhance the likelihood of copulation between the pair. The redirected attack of the male might have become established as the prelude to copulation – a ritual in which the male communicates to the female that he is ready for copulation and which arouses the female so that she is physiologically receptive for copulation. Those approaches, postures and colours which most efficiently effect the communication and arouse the female would be kept and others discarded (by natural selection), until a stereotyped innate pattern became adopted in time. It is remarkable, but not unexpected, that almost the same postures, approaches and colours are most efficient for both sexual arousal and for intimidation of conspecifics. Thus aggression, which under certain circumstances results in mutual repulsion, has acquired a new function – that of attraction. It has been channelled into harmless but useful outlets as in territorial behaviour and courtship, and by means of it the formation of a bond has been made possible. The strong hierarchical tendencies of *A. atra* should be taken into account when housing these lizards for experimental studies. Rock pyramids, sufficient space, and refuges for subdominant individuals must be provided. Potentially combative groupings, such as dominant male + dominant male, should be avoided in confined areas as aggressive reactions and maintenance of individual distance would affect behaviour. Conversely, isolation from the group is likely to result in abnormal behaviour if learning or adaptation is dependent on social stimulation in a social species.

TEMPERATURE PREFERENCES

Introduction

Diel behaviour patterns in *A. atra* are temperature-controlled; very little activity takes place at night or on cold days, whereas the lizards are particularly active at midday in warm weather. Preliminary field observations are presented below on the minimum and preferred air temperature requirements of *A. atra* for different activities. The laboratory observations served to show that *A. atra* has different preferred temperatures under different acclimation conditions and that body temperatures may be increased or decreased by behavioural means. The accuracy of temperature perception is also indicated.

Field observations

Air temperatures on Gunfire Hill were monitored using maximum-minimum and standard thermometers in a Stevenson screen placed in the habitat. Observations were made over 12 days on the activities performed by *A. atra* at different air temperatures.

The lowest air temperature at which activity was noted was 16,3°C, but most lizards only appeared at 17,5–18°C. About 80 percent of the lizards in a particular area had moved into the open and commenced basking at 19°C. Feeding started at 19–20°C. Air temperatures were rarely high enough to cause the lizards to seek shade and dominant males often maintained their position on a display post at air temperatures in excess of 26°C.

Laboratory observations

An apparatus which allowed a choice of temperature zone with minimal interference from other factors such as light, humidity and observer disturbance, was placed in the vivarium. The apparatus consisted of a 1R 240–250W infra-red lamp, a sheet of softboard 1,5 × 1 m on which concentric circles were drawn and a six-probe electronic thermister. The lamp was suspended 8 cm above the centre of the board, and was sufficient to prevent the lizards from positioning themselves directly beneath it without overheating, but not too high to allow comfortable occupation of the circled area of the board. When the lamp was switched on, the lizards rapidly positioned themselves on the board in their preferred temperature zone. In control experiments, lizards were not attracted onto the board surface when the lamp was not switched on.

Thermister probes penetrated the board from below and protruded 4 mm above its surface, one in the circumference of each concentric circle. The temperature gradient was monitored remotely on an electronic thermister meter. The gradient established ranged from 55±2°C in the centre to 25±2°C in the outside circle. The apparatus is similar to that used by De Witt (1967).

Observations were made between 08h00 and 23h00 on seven lizards (D, F, H, I, J, K, L: Table 4). Individual observations were usually separated by a period of more than 30 minutes. The time, lizard's name and positional temperature were noted in each case, as well as the posture, orientation and group position of the lizard. Two postures were distinguished, alert and relaxed, and two orientations, facing the lamp or facing to one side.

Two series of experiments were conducted – one with the air temperature in the constant temperature room at 26,5±2°C and the other at 29,4±1°C. Acclimation periods of 12 and 6 hours respectively were allowed before readings commenced in each experiment. Relative humidity fluctuated between 46 percent and 49 percent as recorded on a thermohygrograph in the room.

Series 1: *Lizards acclimated at 26,5±2°C.* Three hour-long observations revealed the following typical behaviour pattern: a lizard emerged from underneath the board and moved to the above-40°C zone, heated up briefly in the alert position, then moved to the below-40°C zone, where it adopted the lateral posture and shuffled around until the preferred temperature zone was found.

A total of 152 positional temperature readings was taken over five days. The lizards showed a pronounced preference for the temperature zone 32–34,9°C (Figure 2A). The mean of all readings was 34,3°C. The highest positional temperature recorded was 46°C (momentarily) and the lowest 28°C. No panting was observed.

On 10 occasions, lizards were seen to occupy positions at temperatures above 40°C. On all these occasions they were observed to be in the alert position, *i.e.* with the head and shoulders up and forelegs stretched, facing the source of heat. This attitude is characteristic of lizards in the field which temporarily occupy positions with temperatures which would result in overheating (De Witt 1967).

Two additional groups of lizards were tested. The first group consisted of an adult male, a female and a juvenile. The adult female took up a position at 35°C and then over the following two hours shuffled back slowly to 30°C. The adult male remained restless and alert, constantly moving from one position to another. The juvenile constantly adjusted its position when the male moved, maintaining an individual distance of about 7 cm from the male. The juvenile was occasionally forced into suboptimal zones by this behaviour, but when undisturbed by the male, chose a position near the female but at a lower temperature. Positional temperature readings were taken every 15 minutes for six hours. Temperature preferenda were: male 32°C, female 33°C and juvenile 30,8°C.

The second group consisted of an adult female and two juveniles. The lizards always remained in a compact group, the juveniles following the female. The female remained alert, made occasional rapid excursions around the board and appeared to be playing a protective role. The group initially occupied a position at 37°C, and then shuffled back to 33,5°C. Temperature preferenda were: adult female 35,2°C, juvenile female 34,2°C and juvenile male 33,8°C.

Both group experiments indicate that thermoregulatory behaviour may be affected by social status, an observation confirmed in the field where juveniles may occupy suboptimal areas while avoiding adult males. In both experiments the behaviour of juveniles was affected by the movements of the adult female; in the first the adult male had an additional effect. The adults both moved into suboptimal areas during their excursions around the board. De Witt (1967) noted in the desert iguana *Dipsosaurus dorsalis* that body temperatures are permitted to rise well above the preferred level during protective behaviour in the presence of predators.

Series 2: *Lizards acclimated at 29,4°C.* A total of 72 positional temperature readings was taken over six days. The lizards showed a general preference for the temperature zones 35–43,9°C (Figure 2B). The mean of all readings was 37°C.

Pre-chilled and preheated lizards.

Lizard 'L' was pre-chilled in a cold room at 8°C for 10 minutes. Immediately before introduction into the thermal gradient, cloacal temperature was measured at 23°C. The lizard remained in the position in which it was placed (the outer concentric circle) for the first 40 minutes of the experiment, then over a period of 16 minutes moved inwards from 27,5° to 34°C where it remained for 10 minutes in the alert position with mouth open. Thereafter it assumed a broadside posture in the 31,5°C zone and remained there until the conclusion of the experiment. Cloacal temperature rose 16,5°C to 39,5°C in 66 minutes.

The experiment was repeated three days later using the same lizard. After 50 minutes of inactivity the lizard moved to the 33°C zone, assumed an alert posture at 37°C and finally rested in the broadside posture at 30,5°C. Cloacal temperature increased from 21°C to 34,5°C

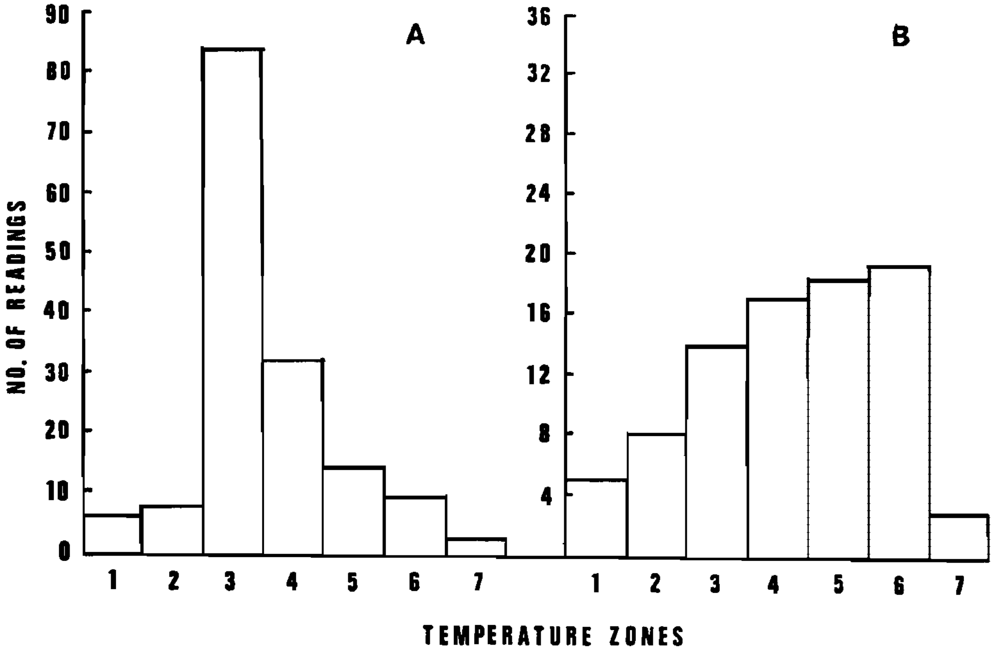

FIGURE 2

Temperature preferences in a concentric thermal gradient of *A. atra* acclimated at 26,5±1°C (A) and 29,4±1°C (B). Temperature zones are: 1–26 to 28,9°C; 2–29 to 31,9°C; 3–32 to 34,9°C; 4–35 to 37,9°C; 5–38 to 40,9°C; 6–41 to 43,9°C; 7–44 to 46,9°C.

in 70 minutes. Lizards in the field were also found to increase cloacal temperatures by basking in the alert and broadside positions on prominent rocks throughout the day, but especially in the morning.

A. atra is clearly able to raise body temperatures rapidly by behavioural means, and and reacts to ambient temperatures until a preferred body temperature is attained. Behavioural thermoregulation (involving movement relative to the heat source, as well as orientation of the body) may be assisted by physiological adjustments, *e.g.* venous shunts of blood to the head sinuses as demonstrated by Bartholomew & Tucker (1963) in the agamid *Amphibolurus barbatus* and Heath (1966) in horned lizards, but this was not investigated in *A. atra*.

Another lizard (H, Table 4) was placed in a box at an air temperature of 57°C for ten minutes. When introduced onto the thermal gradient, the lizard moved rapidly around the outside of the board, and exhibited an ultramarine dewlap and raised nuchal crest. A position at 35°C was eventually chosen. Cloacal temperature dropped from 39° to 37°C in 50 minutes.

In a second experiment the lizard remained for an hour at 30,5°C and then settled at 35,5°C. Cloacal temperature dropped from 39° to 36,1°C in 70 minutes.

Pre-warmed lizards thus reduced body temperatures by remaining in cooler zones on the board, thereafter selecting the preferred temperature zone.

Discussion on thermoregulation

In the field *A. atra* was usually active at air temperatures above 19°C. In Grahamstown the mean daily maximum air temperature exceeds 19°C in all months except June (Geography Department, 1969) and normal activities take place on sunny days almost throughout the year. Mean daily minimum temperatures are below 15°C throughout the year, and little nocturnal activity is likely to occur; none was witnessed in the field. Temperature was the controlling factor as lizards maintained under light conditions of 12 hours light and 12 hours dark and at a constant temperature of 32 ± 1°C exhibited more nocturnal activity than lizards in the same light regime and habitat but at ambient temperatures.

Cowles (1940) divided ectothermal lizards into two groups: thigmotherms which gain heat by conduction from the surrounding environment (air, soil, water, etc.) and have low body temperatures, and heliotherms, or sun-basking lizards, which gain heat by absorbing radiant energy and have high body temperatures. *A. atra* fits the latter category.

Thigmothermic lizards are passively dependent on environmental temperatures and consequently behavioural mechanisms play a small role in thermoregulation. In contrast the heliothermic species are active and accurate behavioural thermoregulators. As their preferred body temperature is high they must select a warm substrate and bask to raise the body temperature, and when the thermal ceiling is reached they must actively seek shade. Thus the heliothermic lizards, by maintaining a thermal plateau when environmental temperatures allow, more closely approximate the homeothermic condition. Their high temperature requirements, however, preclude activity when temperatures fall below a certain minimum, and as a result these lizards are mainly active during the day. *A. atra* maintained in an artificial environment (and with the thermal history of those collected in Grahamstown) should have a temperature regime with maxima above 19–20°C, the level beyond which they can elevate their body temperature by behavioural and other means to the preferred temperature plateau. Higher maxima would result in a quicker attainment of the preferred temperature plateau or higher preferred body temperatures, and more activity.

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