

## On the Role of Colour Display in the Social and Spatial Organization of Male Rainbow Lizards (*Agama agama*)

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**Abstract.** A population of rainbow lizards (*Agama agama*) was studied in central Kenya. Rainbow lizards are able to rapidly change their colours. Dominant territorial males usually exhibited intensive bright colours. Dominant males were less intensively coloured when close to their territory border than in its center. Dominant males tolerated subordinate adult males in their territories. The colours of subordinate adult males were less intensive when these males were close to dominant males than when far from them. We interpret our findings in light of theories of sexual selection.

### Introduction

Social communication in animals takes a variety of expressions, auditory (e.g. bird song (Payne, 1983) and frog call (Wells, 1977)), olfactory (e.g. scent marking in mammals (Erlinge et al., 1982), and visual (e.g. lizard head "bobbing" (Carpenter, 1967)). These signals have functions in the social and spatial organization of populations. Two functions that usually can be distinguished, although the concepts tend to intermingle, are male competition and female choice (provided that the females are the sex in short supply in the species considered). A clear cut categorization can be made if males, by intimidating or outwitting other males, get access to females that do not oppose mating *or* if males are chosen by females on basis of their qualities. These qualities may be genetic and possibly assessed by females on basis of some kind of display or they may constitute the possession of some kind of resource or skill that is offered to the female if the particular male is chosen (Andersson, 1982).

Agamid lizard communication has some peculiar aspects that make them excellent subjects for studies of social behaviour. Their repertoire of communication includes "head bobbing", "push up's", fighting, and colour display (Harris, 1964). Male colours form a gradient from grey, over the typical female "green spotted head" colour, increasingly red head colour to the display of magnificence by a dominant male with bright red head and intensive blue and green colours on body and tail. Female colour

repertoire is much less spectacular, ranging from totally grey-brown to brown with red stripes laterally and green spotted head (Harris, 1964 and pers. obs.).

Intersexual colour dimorphism that is related to colour display and mating behaviour is well known in vertebrates (e.g. Hamilton and Zuk, 1982). Many species of the family Agamidae have, in contrast to most other vertebrates, the ability to rapidly change their colours (within a minute) (Stamps, 1977), thus reflecting the short term optimum message to convey. To the benefit of the observer, their message (or at least its physical expression) is easy to observe and record.

In 1964 Harris published a monograph of his studies of the rainbow lizard (*Agama agama*) in Nigeria. In this report we concentrate on the role of colour display in the social and spatial organization of the rainbow lizard, aspects not fully covered in Harris' (1964) study.

### Study area

The study was conducted in Kora game reserve in central Kenya (0° 5'S, 38°40'E). Rainbow lizards in this area have a rather patchy distribution. Populations are found in two different habitats; along the Tana river and on rocky outcrops and inselbergs. The study area was approximately 50 × 100 m. It was situated at a camp site that was erected on the river bank.

### Methods

The study was conducted from 14 December 1983 to 16 January 1984. 24 rainbow lizards were seen on the study site. 23 (14 males and 9 females) of these were captured. Captures were made by noosing, using a nylon sling on a three meter long bamboo rod. The lizards were sexed on basis of femoral pores (present on males, Harris, 1964), and permanently marked by toe-clipping. We also painted a number on their backs; this permitted individual identification from a distance.

Observations were carried out while walking through the study site in bouts, on average 7 bouts per day, each lasting about 30 minutes. One to 17 lizards (mean 8.9) were identified on each bout. The study area was divided into 97 subareas that, together with 94 objects, were used to register the position of observed lizards. Home range sizes were computed from the maximum convex polygon. The estimates were based on 19 to 139 sightings (mean 72). We also noted the colour of all observed lizards. Colours were classified as brown/grey", green spotted head", "red cheeks", "red", and "cock colour". Males that throughout the study period were seen in one color phase ("green spotted head") were considered subadults. (These were less than 9 cm in body length). Males seen changing colours but rarely seen in cock colours were considered as subordinate adults (these males were more than 9.5 cm sv.). A territorial adult male is one that usually appeared in cock colours. These are here termed cock

males (Harris, 1964). Fights and courtship were recorded whenever observed. Scats were collected at roosts that were used by both males and females.

Two cock males were temporarily removed in order to observe changes in social and spatial organization.

## Results

### *Body size, spatial organization, and diet*

Males were larger than females ( $x = 10.9$ , S.D. = 2.6,  $N = 14$ ;  $x = 7.9$ , S.D. = 2.1,  $N = 9$ ;  $t = 2.90$ ,  $P < 0.01$ ). Cock males were larger than subordinate adult males ( $x = 13.6$  cm, S.D. = 0.8,  $N = 5$ ;  $x = 10.8$  cm, S.D. = 1.4,  $N = 7$ ;  $t = 4.01$ ,  $P < 0.001$ ).

The home ranges of males (all categories) were larger than those of females (males:  $x = 556$  m<sup>2</sup>, SD = 330,  $N = 12$ , MNO (mean number of observations per home-range) = 70; females:  $x = 197$  m<sup>2</sup>, SD = 144,  $N = 9$ , MNO = 76;  $t = 3.21$ ,  $P < 0.01$ ). The home-ranges of cock males were not larger than those of subordinate adult males (dominant:  $x = 475$  m<sup>2</sup>, SD = 331, MNO = 52,  $N = 4$ ; subordinate:  $x = 697$  m<sup>2</sup>, SD = 233,  $N = 7$ , MNO = 76).

The home-ranges of cock males overlapped female and subordinate male home-ranges (Figs. 1 and 2). The home-ranges of cock males were non-overlapping (Figs. 1-2). Eight of the nine females marked on the study site had overlapping home-ranges (Fig. 1). Also home-ranges of subordinate males (both adult and subadult) overlapped.

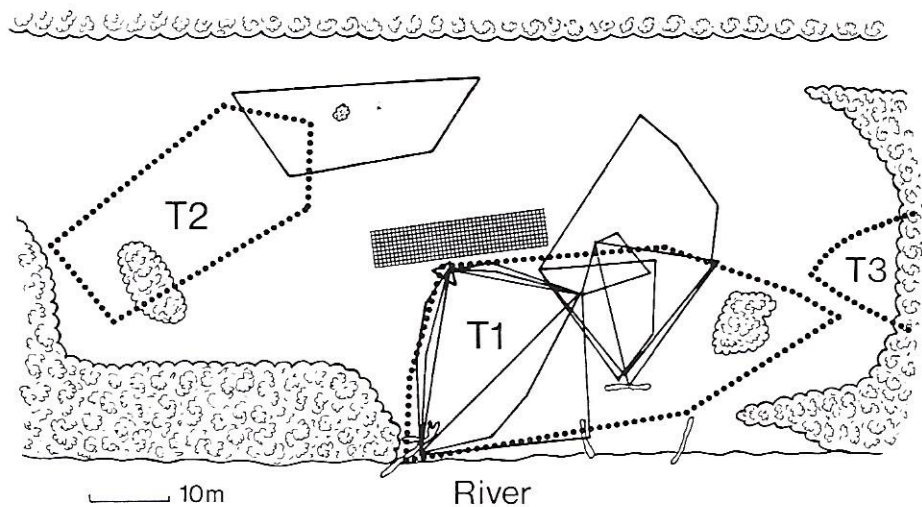
The analyzed scats ( $N = 50$ , from both males and females) contained mainly ants.

### *Removal experiments*

During the eight days before any removals were performed the study site was occupied by three cock males (no. 18, 22 and 21 in territories 1, 2, and 3 respectively, Figs. 1 and 2). No aggressive behaviour was observed between these three males.

After the removal of the first cock male (no. 22) his previous territory was occupied by two males. One of these was a former subordinate (no. 4) in male no. 18 territory (Fig. 2) and the other male (no. 23) moved in from an area outside the study site. When no. 22 was reintroduced, he was attacked by male no. 4 and was unable to retake all of his former territory.

In the second experiment male no. 18 was removed. The vacant territory was for the first five hours occupied by male no. 21. He had previously been observed as a cock male in the outskirts of the study site (Figs. 1 and 2). Later male no. 4 left his territory taken from male no. 22 and moved into the territory now occupied by male 21. This resulted in a fight which, in turn, resulted in the division of the territory between the two males. When reintroduced, male no. 18 was not able to retake his former territory and after a fight with male 4 he was never more seen in cock colours.



**Figure 1.** Female home ranges (continuous lines) and male territories (T1 - male 18, T2 - male 22, T3 - male 21) prior to the removal experiments. Logs, a house, and bushes are also shown.

#### *Colour changes in males*

In the majority of observations (80%,  $N = 240$ ) of cock males, these were in cock colours. The colours of subordinate adult males varied and were affected by the distance to the nearest cock male. They were most colourful when far from cock males (Table 1). Subadult males were only observed in the "green spotted head" phase and their colours were thus not affected by the distance to a cock male.

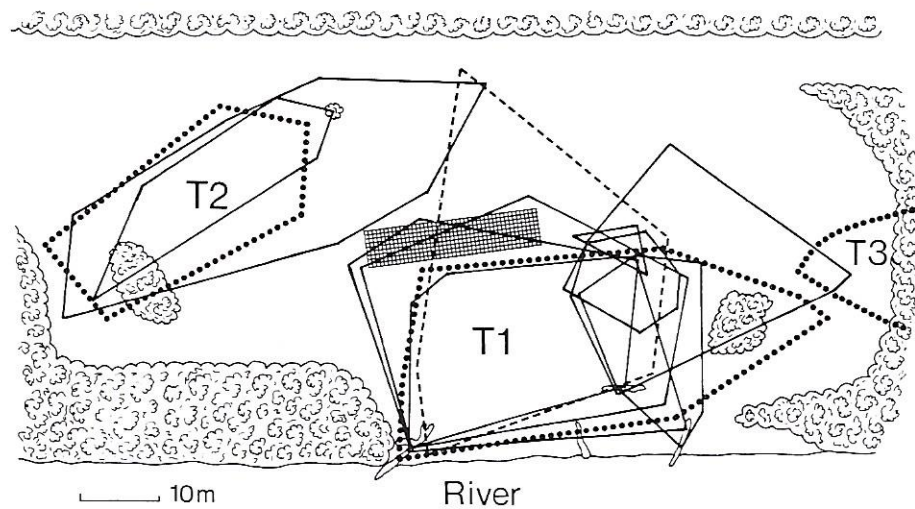
Cock males were significantly more often displaying their cock colours in the centre of their territories (85% of all observations,  $N = 193$ ) than along the territory borders (57%,  $N = 47$ ;  $\chi^2 = 16.86$ ,  $P < 0.001$ ).

Only males in cock colours were seen courting females. Courting was observed on 11 occasions. In ten of these it was performed by a cock male and in one by a subordinate adult male, in cock colours.

#### **Discussion**

##### *Home-range size*

As in many other studies on lizard spatial organization (e.g. Turner et al., 1968) we found that males occupy larger home ranges than do females (Fig. 1). Males grow larger than females but also males that were smaller than some of the females occupied larger home-ranges than these. Both sexes fed on the same kind of food (ants). Thus, as suggested by Stamps (1983), the difference in home range size is most likely not related to energy requirements. Cock males could increase their reproductive success by in-



**Figure 2.** Subordinate male home ranges. The dashed line denotes the home range of male 4 when he was a subordinate prior to the removals.

cluding as many females as possible in their territories, even if these territories were oversized with respect to the energetical optimum. This could well explain why they have larger home-ranges than females. However, also subordinate males, that most likely never reproduce, have larger home-ranges than females. It could be that it is important for subordinates to be acquainted with a large home-range to increase their possibility to take it over, should the local cock male disappear. Also information on the situation in neighbouring territories could be important in permitting future take-over of these. That a subordinate male is able to take over a neighbouring territory when a cock male disappears was confirmed during the removal experiments.

#### *Removal experiments*

The cock males' territories were non-overlapping which suggests that they had the character of territories. This interpretation is supported by the outcome of the removal experiments when vacant cock home ranges almost instantly were reoccupied by neighbouring cock males or, in one instance, by a subdominant adult male that gained cock status.

#### *The function of cock colours in male social and spatial organization*

Subordinate adult males were constantly changing their colours and they became more colourful when they were far from cock males than when they were close. Visual contact appears to be sufficient to make a subordinate change into duller colours since no attacks by dominants on subordinates were seen. Only males in cock colours were

**Table 1.** Distance from the nearest cock male and its effect on the colours of the nearest subordinate adult males.

Colour of subordinate adult males	Distance to nearest cock males (meters)	SD	N
“Grey/brown”	8.5	4.7	87
“Green spotted head”	7.8	4.5	88
“Red cheeks”	10.1	4.2	105
“Red”	11.3	5.1	24
“Cock colour”	13.7	5.8	6

observed courting females. Our study is too short to exclude the possibility that males in dull colours occasionally court females. However, if they do so only rarely this suggests an explanation to the fact that subordinate males are tolerated in territories. By controlling the subordinates' colour the territorial male also largely controls their mating possibilities without excluding them from his territory.

The fact that cock males reduced their display at the territory border suggests that it also functions in male-male interactions. In other species of territorial lizards it has been found that the males' aggressive response to intruders is most frequent in the center of the territory (Yedlin and Ferguson, 1973).

It is very difficult, both conceptually and in the field, to separate male competition and female choice when explaining animal behaviour. This is especially evident in a short observational study. However, the most simple interpretation of our results involves aspects of both mechanisms.

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