Territoriality and allometry in a population of harduns

*Laudakia stellio* on Rhodes

by

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Summary – Harduns (*Laudakia stellio* (Linnaeus, 1758)) were captured in April and June outside the city of Rhodes. Snout-vent length, weight, head width and jaw length was measured on all 74 individuals. Males were identified on basis of present precloacal glands. Larger males were heavier and had larger heads in relation to body length than females. Twenty nine agamas at a subsite were also painted with numbers visible at a distance and their home ranges were mapped. Some of the adult males were frequently observed. They maintained exclusive home ranges. The home ranges of some, usually smaller, males overlapped each other and those of the males in the first group. Two out of three large territorial males kept their territories from April to June while one (who had lost in weight) was replaced. Also the pattern of female home ranges suggests a tendency to intrasexual territoriality, especially if the smallest females are not considered. The home ranges of juveniles overlapped each other and those of adult males and females. The April juvenile home ranges were particularly large. Open aggression was rare. Only when an apparently strange male entered the study area was he physically attacked.

Keywords: Agamidae, home range, sexual dimorphism.

Résumé – Territorialité et allométrie chez une population d’agames *Laudakia Stellio* à Rhodes.

Les agames (*Laudakia Stellio* (Linnaeus, 1758)) ont été capturés en avril et juin à la périphérie de la ville de Rhodes. La longueur museau-cloaque, le poids, la largeur de la tête et la longueur de la mâchoire ont été mesurés sur 74 individus. Les mâles ont été identifiés sur la base de la présence des glandes pré-cloacales. A l’âge adulte, les mâles sont plus lourds et plus grands et ont des têtes plus larges que les femelles. Dans un sous-site, vingt-neuf individus ont été peints avec des numéros visibles à distance et leurs domaines vitaux ont été cartographiés. Certains mâles adultes ont été fréquemment observés. Ils ont maintenu des domaines vitaux exclusifs. Les plages d’accueil, généralement plus petites, de certains mâles se chevauchent. Deux grands mâles territoriaux sur trois ont gardé leurs territoires d’avril à juin, tandis que l’un (qui avait perdu du poids) a été remplacé. Le modèle des domaines vitaux des femelles, petites femelles non considérées, suggère une tendance à la territorialité. Les zones d’accueil des jeunes femelles se chevauchent ainsi que celles des mâles et femelles adultes. Durant le mois d’avril, les jeunes femelles étaient particulièrement présentes et le recours à l’agression était rare. Seuls les mâles étrangers sont féroces et attaqués.
I. INTRODUCTION

There has since long been much interest in the social ecology of lizards (Stamps 1983). Most work has however been carried out on North American iguanid species with only few studies on European lizards. Agamids, with an extensive Old world distribution, have conspicuous social behaviours; aggression and courting, which make them convenient study objects in this field of research (Stuart-Fox & Ord 2004). Single species studies have been made of the African Agama agama (Linnaeus 1758) (Harris 1964, Inoué & Inoué 1977, Yeboah 1982, Madsen & Loman 1987) and of Acanthocercus atricollis (Smith 1849, Reaney & Whiting 2003). The only European agamid is the hardun (Laudakia stellio) (Linnaeus 1758). Its reproductive cycle has been described by Childress (1970) (Lebanon) and by Loumbourdis and Kattoulas (1981, 1982, 1985) (Greece). Norfolk et al. (2010) describe its habitat niche in Israel, Dusen and Ord (2001) have studied its diet in Turkey. Such data are basic to further work on the social relations in populations of a species. The present study reports on the spatial relations of lizards in a local population during part of the breeding season. We also discuss some implications of our results for an interpretation of the social relations in the population. More information on this is available for Israeli populations of harduns (Arbel 1980, 1982).

II. MATERIAL AND METHODS

The study was carried out on Rhodes, a Greek island off the south western Turkish coast. The study area, consisting of an ancient stadium with associated ruin structures, is situated in the vicinity of the city of Rhodes on the north part of the island. The place is regularly visited by hordes of tourists. This is probably a reason why the lizards are relatively easy to approach (Labra & Leonard 1999). Presumably there are no other effects on the behaviour of the lizards. Field work carried out April 8 to 12 (five days) and May 31 to June 7 (eight days) 1986. Beginning of April 1986 was unusually warm and sunny while weather in June 1986 was normal (warm and sunny). Harduns were captured in the whole area for meristic purposes. Individual marking making distant identification possible and intensive observations were performed at a subsite; a wall from classical times (Fig. 1). It faced south; on the
north side the ground was level with the top of the wall. The wall was about 6 m high and 140 m long. Only 80 m of length, to the west of a large bush covering some 10 m of wall with deep shade, were studied during April while the full wall was studied in June. There were scattered herbs and small bushes growing on the face of the wall, providing some cover for the lizards. North and south of the wall there was almost no vegetation on the ground, making the wall somewhat isolated as lizard habitat. Positioning the lizards was facilitated by the fact the wall had a system of rectangular holes into the soil behind. The holes were about 15 times 30 cm and located on a regular 1.5 m grid. These holes were used as hides during night and when weather was overcast.

During the first two days of each study period we mainly captured and marked lizards. During the rest of time (two and five days respectively) we mainly observed the location and behaviour of the lizards on the wall, occasionally attempting to capture any unmarked lizards seen. The lizards were captured by noosing. The sex of adult lizards was determined from the presence of precloacal glands (Beutler 1981). They were weighed (“Pesola” dynamometer scale to 1 g), body and tail length measured (ruler to 1 mm) and also head length (snout to end of jaw) and head width (maximum) (using calliper to 0.1 g) and before being release the

Figure 1: Western part of the wall that was the site for the study of marked harduns.
Figure 1 : Partie occidentale du site (mur) d’étude des harduns marqués.
lizards were marked individually by toe-clipping and painted with a large number on their back. They were released within 10 minutes of capture.

The lizards were located while walking back and forth about 20 m from the wall, from the beginning of activity at about 9.00 a.m until it ceased about 17.30 p.m. (April) or 17.00 p.m. (June) (local summer time). The lizards were, if visible, located about once every 20 minutes. More locations were registered if they moved. Unmarked lizard could sometimes be recognized because of distinctive marks, like a broken tail, and also their home range could thus be plotted. Some of these were captured on later days when their sex and weight could be determined. A total of 26 lizards were captured, marked and observed.

There were altogether 347 observations registered in April. Eight of these were of large or medium sized lizards that could not be identified. It is assumed that these represent one, or at most two different animals. Another 12 were of small, unidentified lizards. These probably represented two or three different juveniles, possibly transients. There were altogether 246 observations registered in June. Eleven of these observations were of medium sized or large and nine of small lizards that could not be identified. The observations of large lizards probably referred to two different animals and those of small to at most three different animals.

Home range areas were computed using the convex polygon method. Because they were based on different numbers of observations it was necessary to correct for this. We used the corrections factors supplied by Jennrich and Turner (1969). For N > 25 we extrapolated their figures using a logarithmic smoother (SYSTAT).

Although less intensively, we also searched the surroundings of the wall. The immediate surroundings were a bare sand field and, above the wall, a road. Neither was used by harduns. Only two of the animals regularly observed on the wall, and thus considered on Figs 4 and 5, were ever observed away from the wall. They (#38 and #55) were each seen once in trees about 20 m from the wall.

Below we will classify animals up to 7.9 cm in body length as juveniles and animals 8.0 cm or more in April and 9.0 cm and more in June as adult (Fig. 2). The two animals between 8.0 and 8.9 cm observed in June are not considered further. They were not relocated after capture.

Also, two lizards from Rhodes and eight from the area around Philemos were killed on April 10th and dissected. Size of gonads and of any eggs or follicles was measured.
III. RESULTS

Age classes, allometry and density of animals

The size distribution of individuals in April (Fig. 2) suggests that those below 7 cm in length represent a distinct age class, probably young of the previous year. The size distribution in June suggests that no young had hatched so far during the year of the study. Males were heavier than females (Tab. I, Repeated measures with sex as grouping factor: F = 14.1,

**Table I:** Weights of the specimens in April and in June (broken down by sex and age).
Tableau I : Poids des spécimens en avril et en juin (classés par sexe et âge).

<table>
<thead>
<tr>
<th>Ind. #</th>
<th>Sex/Age</th>
<th>Precloacal glands present</th>
<th>April weight (g)</th>
<th>June weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>F</td>
<td>no</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>F</td>
<td>no</td>
<td>58</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>F</td>
<td>no</td>
<td>52</td>
<td>53</td>
</tr>
<tr>
<td>12</td>
<td>F</td>
<td>no</td>
<td>33</td>
<td>40</td>
</tr>
<tr>
<td>13</td>
<td>F</td>
<td>no</td>
<td>33</td>
<td>38</td>
</tr>
<tr>
<td>14</td>
<td>F</td>
<td>no</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>F</td>
<td>no</td>
<td>52</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>F</td>
<td>no</td>
<td>52</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>F</td>
<td>no</td>
<td></td>
<td>47</td>
</tr>
<tr>
<td>21</td>
<td>F</td>
<td>no</td>
<td></td>
<td>52</td>
</tr>
<tr>
<td>56</td>
<td>F</td>
<td>no</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>J</td>
<td>no</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>J</td>
<td>no</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>J</td>
<td>no</td>
<td>14</td>
<td>16</td>
</tr>
<tr>
<td>24</td>
<td>J</td>
<td>no</td>
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<td></td>
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<tr>
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<td>J</td>
<td>no</td>
<td></td>
<td>15</td>
</tr>
<tr>
<td>47</td>
<td>J</td>
<td>no</td>
<td></td>
<td>20</td>
</tr>
<tr>
<td>1</td>
<td>M</td>
<td>yes</td>
<td>72</td>
<td>66</td>
</tr>
<tr>
<td>3</td>
<td>M</td>
<td>yes</td>
<td>60</td>
<td>75</td>
</tr>
<tr>
<td>4</td>
<td>M</td>
<td>yes</td>
<td>59</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>M</td>
<td>yes</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>M</td>
<td>yes</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>M</td>
<td>yes</td>
<td></td>
<td>40</td>
</tr>
<tr>
<td>38</td>
<td>M</td>
<td>yes</td>
<td></td>
<td>74</td>
</tr>
<tr>
<td>55</td>
<td>M</td>
<td>yes</td>
<td></td>
<td>95</td>
</tr>
<tr>
<td>60</td>
<td>M</td>
<td>yes</td>
<td></td>
<td>56</td>
</tr>
</tbody>
</table>
There was no significant change in weight from April to June (Repeated measures: F = 1.17, d.f. = 1:3, P = 0.36). Actually, one male lost weight during this period.

Among the dissected lizards, four above 7.8 cm in size (snout-vent) had obvious ovaries. The largest eggs were 7 mm in size. None of these had precloacal glands. Three large lizards (12.9, 12.3 and 10.6 cm) with precloacal glands had obvious testes. Three lizards below 6.9 cm lacked precloacal glands. The gonads of the largest of these were probably testes while the sex of the two smaller was not obvious (Tab. II).

Lizards with precloacal glands, assumed to be males, had relatively larger heads than others (Fig. 3). The difference grew more marked the larger the lizards were.

These findings support our classification into males, females and juveniles (Tab. I).

Excluding transients but including non-marked animals judged to be present we estimated the total April population (living on about 500 m$^2$ of wall face) to five males, nine females,
and five juveniles. The total June population (on about 700 m² of wall face) was eight males, 11 females and six juveniles.

**Behavioural notes**

There was no obvious colour dimorphism. Only one case of physical aggression was observed. This took place when an unmarked, apparently new, male appeared in the home range of another male. The ”intruder” was bitten in the head by the resident male and later also chased a comparatively long distance.

There were three observations of males nodding at each other. There were eleven instances when a male and a female nodded at each other. Usually nothing more happened or the female moved away when the males approached (five cases). One instance of more intense courtship (?) was observed (in June), the male biting the side of a female. There were three cases of one female being chased away by another. On the whole, the scene was rather lazy.

<table>
<thead>
<tr>
<th>Body size (s-v) (cm)</th>
<th>Presence of precloacal glands</th>
<th>Gonad size (left + right) (mm)</th>
<th>Eggs / follicles, max. size</th>
</tr>
</thead>
<tbody>
<tr>
<td>12.9</td>
<td>yes</td>
<td>10.5 + 12.0</td>
<td>none</td>
</tr>
<tr>
<td>12.3</td>
<td>yes</td>
<td>12.2 + 14.5</td>
<td>none</td>
</tr>
<tr>
<td>10.6</td>
<td>yes</td>
<td>12.5 + 10.3</td>
<td>none</td>
</tr>
<tr>
<td>10.7</td>
<td>no</td>
<td>22.0 + 23.0</td>
<td>7 mm</td>
</tr>
<tr>
<td>10.0</td>
<td>no</td>
<td>10.0 + 11.0</td>
<td>not measured</td>
</tr>
<tr>
<td>8.0</td>
<td>no</td>
<td>5.5 + 5.0</td>
<td>2 mm</td>
</tr>
<tr>
<td>7.8</td>
<td>no</td>
<td>5.0 + 5.0</td>
<td>2 mm</td>
</tr>
<tr>
<td>6.9</td>
<td>no</td>
<td>2.1 + 2.0</td>
<td>none</td>
</tr>
<tr>
<td>5.3</td>
<td>no</td>
<td>1.5 + 2.0</td>
<td>none</td>
</tr>
<tr>
<td>5.0</td>
<td>no</td>
<td>1.5 + 1.5</td>
<td>none</td>
</tr>
</tbody>
</table>
Home range sizes

There was no difference in average home range size between males and females (average for April and June area used; $t = 0.34$, d.f. = 16, $P = 0.72$) (Fig. 4). There were no significant correlations between lizard size and home range area (Males April: $r = 0.74$, d.f. = 4, $P = 0.15$; Males June $r = 0.46$, d.f. = 4, $P = 0.44$; Females April: $r = 0.14$, d.f. = 5, $P = 0.79$; Females June: $r = 0.02$, d.f. = 8, $P = 0.96$).

Figure 3: Relative head size of harduns. “Males” are animals with precloacal glands. “Females” and “Juveniles” are separated on basis of the size distribution gap.

Figure 3 : Taille relative de la tête des harduns “Mâles” avec des glandes pré-cloacaux. “Femelles” et “juvéniles” sont séparées sur la base de l’écart de distribution de taille.

Figure 4: Home range sizes (m$^2$). Sizes are computed with the convex polygon method and corrected for sample size.

Figure 4 : Tailles des zones de tolérance (m$^2$). Les tailles sont calculées avec la méthode du polygone convexe et corrigées pour la taille de l’échantillon.
April home range patterns

The three largest males (#3, #1 and #4) had distinctly abutting home ranges (Fig. 5a). Two smaller males (#5 and #6) had overlapping home ranges that were on the border between two of the larger males’. The smaller males were not observed as many times as the larger ones. This could mean that they moved more in cover while the larger ones preferred to display their presence.

Apart from #13 and #12, who were small, also the home ranges of the females (#16, #X, #11, #14, #7) were almost nonoverlapping (Fig. 5b). #17 was a large female but partly overlapped #11.

Figure 5: Locations of marked harduns in April. The shadowing represents the bare ground in front of the wall. a) Males. The body lengths of the males were: 1-11.1 cm, 3-10.5 cm, 4-11.1 cm, 5-9.6 cm, and 6-8.9 cm. b) Females. Their body length were 7-11.0 cm, 11-10.6 cm, 12-8.8 cm, 13-8.9 cm, 14-10.1 cm, 16-10.6 cm, and 17-10.4 cm. Apart from these females one female, 2-10.3 cm, was captured once but not relocated in April. The individual X (with a broken tail) is tentatively considered a female (from its coloration) and its size estimated to about 10 cm. c) Juveniles. Their body lengths were 8-6.7 cm, 9-6.0 cm, and 15-6.7 cm.

Figure 5 : Emplacements des harduns marqués en avril. L’ombre représente le sol nu en face du mur. a) Longueur corporelle des mâles : 1-11,1 cm, 3-10,5 cm, 4-11,1 cm, 5-9,6 cm, et 6-8,9 cm. b) Longueur corporelle des femelles : 7-11,0 cm, 11-10,6 cm, 12-8,8 cm, 13-8,9 cm, 14-10,1 cm, 16-10,6 cm et 17-10,4 cm. Une femelles (2-10,3 cm), a été capturée une fois mais non retrouvée en avril. Avec une queue cassée, elle est considérée comme une femelle (à partir de sa coloration) et sa taille est estimée à environ 10 cm. c) Longueur corporelle des juvéniles : 8-6,7 cm, 9-6,0 cm, et 15-6,7 cm.
One of the juveniles was only observed a few times (during a single hour). The other two had comparatively large, overlapping home ranges (Fig. 5c).

**June home range patterns**

Two of the three large males (#1 and #4) lived in essentially the same home ranges in June as in April. One was only observed (and captured) once in June (#3). His former home range was utilized another, smaller male (#25). This one was captured and observed before the capture of the former male in June. Thus it is not possible that the change of male in the home range was due to the capture stress of the original male. One small male (#60) was only observed a few times, in the home range of another male. He was only observed by the end of the June study period and when he appeared, he was physically attacked and bitten by the resident male. This was the only case of open aggression observed during the study. There were two males (#38 and #55) with nonoverlapping home ranges in the eastern part of the study area, which was only included in June (Fig. 6a).

Most females were in the same home ranges in June and in April. #14 and #12 seemed to have switched place and the small #12 definitely had an exclusive home range in the area formerly occupied by #7 who seemed to have disappeared in June. #17 (who had also moved) and #13 had still home ranges overlapping those of other females. The small #2 was never recaptured in April but had now reappeared and her home range overlapped that of several others. It is doubtful if one can consider the pattern of female home ranges nonoverlapping in June (Fig. 6b).

The juvenile home ranges were smaller in June than they were in April. Two of them overlapped in the preferred western part of the study area (Fig. 6c).

**Figure 6:** Locations in June. The eastern part of the wall is shown on the lower part of figure. a) Males. The body length of the males were 1-11.3 cm, 3-10.9 cm, 4-11.1 cm (measured in April), 25-9.7 cm, 38-11.8 cm, and 55-12.2 cm. b) Females. Their body length were 2-10.3 cm (measured in April), 11-10.6 cm, 12-9.6 cm, 13-9.6 cm, 14-10.1 cm (measured in April), 16-10.6 cm (measured in April), 17-10.4 cm (measured in April), and 56-10.6 cm. c) Juveniles. Their body length were 24-7.4 cm, 26-6.6 cm, and 47-7.6 cm.

**Figure 6 :** Localisations en juin. La partie orientale du mur est indiquée sur la partie inférieure de la figure. a) Longueur corporelle des juvéniles mâles : 1-11,3 cm, 3-10,9 cm, 4 - 11,1 cm (mesurée en avril), 25-9,7 cm, 38-11,8 cm, et 55-12,2 cm. b) Longueur corporelle des femelles: 2-10,3 cm (mesurée en avril), 11-10,6 cm, 12-9,6 cm, 13-9,6 cm, 14-10,1 cm (mesurée en avril), 16-10,6 cm (mesurée en avril), 17 - 10,4 cm (mesurée en avril), et 56-10,6 cm. c) Longueur corporelle des juvéniles : 24-7,4 cm, 26-6,6 cm, et 47-7,6 cm.
IV. DISCUSSION

Our conclusion that the presence of precloacal glands can be used as a sex character in *L. stellio* agrees with the conclusion of Baig and Böhme (1991) and Almog et al. (2005). However, in other related species this may not be true (Baig & Böhme 1991).

The main breeding season of the hardun is probably in the spring. Childress (1970) found a maximum count of motile sperm in vas deferens in March to May when studying the species in Lebanon. Oviductal eggs were found from May. No females had apparently oviposited in June when the study was completed. During the present study only one case of obvious courtship was observed (in June). We conclude that both study periods fell during the breeding period, June possibly being towards its end.

The patterns suggest that large males and large females maintain intrasexually exclusive home ranges, territories. The pattern is more clearly so interpreted for males than for females. The fact that the territories are maintained without open aggression, except when an apparently new male appeared suggests that the animals can recognize each other individually.

The population studied by us largely corresponds to what Arbel (1982) has termed a community of harduns. However, it is clear that despite the high density of the population, there were several territorial males present.

The data from this study are not extensive enough to warrant much speculation on the cause of the patterns observed. However, male territoriality is often interpreted as a caused by competition for females. The fact that the males in the eastern part of the study area had small, not abutting, territories and that this area had the least number of females, only one, may give some support to such an interpretation. Also female competition is indicated by the pattern of female home ranges. Female territoriality has also been noted by Schmidt and Inger (1957, cited in Baig & Böhme (1991). The relatively larger heads found in this study and by others (Cheatsazan et al. 2006, 2008, Aghili et al. 2010) can be interpreted as an indication that male competition is more important than female competition.

V. CONCLUSION

During the study period, April and June, large adult harduns, both males and females, tend to stay in restricted home ranges, up to 500 m² but usually less. Within each sex these
home ranges tended to be exclusive. Males were larger than females. They also had larger heads relative to body length. This difference was greater the larger the animals were.

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**REFERENCES**


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A specimen of hardun from Rhodes, June 1986. The lizard was painted during the first study week and is now shedding. You can also see it was toe clipped. Picture: J. Loman.

Un spécimen d’Agame de Rhodes, juin 1986. Le lézard a été marqué à la peinture lors de la première semaine d’étude et il est actuellement en mue. Vous pouvez également noter le marquage par amputation d’orteils... Photo : J. Loman.