The Ontogeny of Spatio-Temporal Tactics and Social Relationships of Adult Male Iberian Rock Lizards, *Lacerta monticola*

Pedro Aragón*†, Pilar López† & José Martín†

*Laboratoire d’Ecologie, CNRS-UMR 7625, Université de Paris VI, Paris, France; †Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

Abstract

Behavioural aspects of many species may change through their ontogenetic trajectory. Mature males of the lizard *Lacerta monticola* present two types of colour phase, with bright green males being older, larger and more dominant than dull brown males. We hypothesized those ontogenetic differences in males’ competitive ability may lead to differences in spatio-temporal tactics. In a field study, we did not find differences in the size of the home ranges or core areas of green and brown males. However, after controlling for size, green males had more exclusive areas than brown males. Green males also had higher levels of conspicuous activities than brown males. Green and brown males had different spatio-temporal tactics within the day; green males used their home ranges more, were more active and had a higher degree of overlap with other males in the morning than in the afternoon. Brown males did not show these variations through the day. Green males participated in, and won more intrasexual agonistic interactions. Also, green males overlapped more extensively with areas of potential mates, and guarded females more often than brown males. These behavioural differences between males showed plasticity through ontogeny in the use of space, time and types of activity.

Correspondence: Pedro Aragon, Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, E-28006 Madrid, Spain. E-mail: paragon@mncn.csic.es

Introduction

Males of many species exhibit alternative tactics depending upon age and/or local social conditions (Dominey 1984; Moore 1991). These individual differences may be selected because some behaviour patterns may be adaptive at one life stage, or under one set of local conditions, but disadvantageous during others (Baird & Timanus 1998). For example, a high density of conspecifics may result in
intense competition for accessing resources such as potential mates (for theoretical models, see Brown 1982; Schoener 1983 and for experimental demonstrations, see Stamps 1984; Kwiatkowski & Sullivan 2002). In this case, individuals with high social status are more likely than low-status individuals to defend their home ranges against intruders (e.g. Stamps & Eason 1989).

Social status is often closely linked with age, and individuals may move through different behavioural developmental positions along an ontogenetic trajectory (Wiley 1981, Baird et al. 2003). The study of such ontogenetic trajectories, therefore, is essential for understanding not only the evolution of the social systems, but also intraspecific relationships. Because the balance between the costs and benefits of defending territories is expected to change as a function of competitive ability, then the social relationships among males is expected to be influenced by size and/or age.

Resource partitioning by means of shifts in the daily activity patterns of individuals has been recently demonstrated as a way to reduce intraspecific competition in fishes (Alánára et al. 2001). In lizards, not only activity but also inactivity provides benefits (Simon & Middendorf 1976; Rose 1981; Adolph & Porter 1993; Martín & Salvador 1995; Martín & López 2000). Therefore, in contrast to what was reported in earlier studies (Porter et al. 1973), lizards are not always active when the thermal conditions are favourable (Aragón et al. 2001a; Baird et al. 2001). Activity patterns of a given individual should reflect the balance between the costs and benefits of activity vs. inactivity (Martín & López 2000).

Most studies of lizards have analysed only the average daily and seasonal patterns of activity (Rose 1981; Beuchat 1989; Martín & Salvador 1995; Aragón et al. 2001a), which may explain only a part of a lizard’s adaptive strategy. It remains largely unknown how individual variations in activity level within a day are related to changes in intraspecific spatial relationships. We predicted that the activity tactic of a male lizard would depend on its ontogenetic stage and associated competitive ability, as the balance between costs and benefits of being active should differ as a function of their social status. Thus, for example, subordinate individuals decrease their activity levels to decrease the cost of social activities (Martín & López 2000).

The Iberian rock-lizard (*Lacerta monticola*) is a small diurnal lacertid lizard found mainly in rocky habitats of some high mountains of the Iberian Peninsula. This is an excellent species in which to examine differences between male age classes because there are two distinct colour phases of sexually mature males, which are stable within the same breeding season. Males have either bright green or dull brown coloration dominating on all of the visible part of the body, particularly on the dorsal regions, whereas females are brown (cf. Pérez-Mellado 1997). Green males tend to be larger and older (see Results), however brown males are sexually mature, based on observations of spermatogenic activity (Elvira & Vigal 1985), courting behaviour, and attempted copulation (see Results). Agonistic encounters between males of both types occur during the mating season and spatial overlap between males’ home ranges is extensive (Martín & Salvador 1997; Aragón et al. 2001a).
If older green males have superior fighting ability because they are larger, they are expected to win the majority of agonistic interactions against brown males (e.g. Olsson 1992; López & Martín 2001). However, males that are frequently engaged in fights might incur greater energetic and survival costs derived from higher activity (Marler & Moore 1988). Therefore, mechanisms for reducing the frequency of costly fights would be favoured by natural selection. Thus, when the outcome of costly interactions is predictable, inferior competitors may avoid such encounters by retreating before a fight occurs (Maynard-Smith 1982; Enquist & Leimar 1983). Coloration may signal a male’s fighting ability in many lizards (Olsson 1994a,b; Sinervo et al. 2000), and may serve as a long-distance status signal (Cooper 1986; Zucker 1994; Martin & Forsman 1999), which must be beneficial for both contenders if it allows them to avoid costly interactions. In addition, in some species, young, but sexually mature, males may delay the development of nuptial coloration until further breeding seasons (Díaz 1993; Olsson 1994b; Martín & Forsman 1999). Behavioural and ecological differences between these ontogenetic colour phases and their significance have received little attention in lizards (Cooper & Greenberg 1992).

We conducted a field study to examine differences between the two colour phases (i.e. age classes) of adult male *L. monticola* in competitive ability, activity, and in the extent to which they used exclusive areas. Furthermore, we examined the daily variation in the time spent moving and distance travelled, and the allocation of time to conspicuous and non-conspicuous activities.

**Methods**

**Study Site and General Methods**

Field work was conducted from May to Jun. 1998, 1999 and 2000 at ‘Alto del Telegrafo’ (Guadarrama Mountains, Central Spain) at an elevation of 1900 m. Patches of large granite rocks and scree interspersed by shrubs (*Cytisus oromediterraneus* and *Juniperus communis*) were dominant at the study site, together with meadows of *Festuca* and other grasses (Martín & Salvador 1992). The subspecies *L. monticola cyreni* occurs in the study area where it inhabits a relatively limited area on mountaintops between 1750 and 2350 m elevation. Lizards are active from May to Oct., mating occurs from May to Jun. and females produce a single clutch in Jul. (Elvira & Vigal 1985).

The field study was conducted on a 0.2 ha plot (50 × 40 m) that was divided into 20 quadrants of 10 × 10 m each to form a grid. This plot size allowed us to differentiate between residents and transients by monitoring the activity of lizards closely (Rose 1982). Residents were defined as those individuals with more than three sightings in different days, and at least two sightings separated by at least 15 days, over the duration of the entire study. All lizards (58 males and 44 females) were captured by noosing, weighed with a pesola spring scale (males: $\bar{x} \pm 1$ SE = 8.2 ± 0.2 g, range = 5.7–10.0 g; females: 7.9 ± 0.2 g, range = 6.5–9.5 g) and their snout-to-vent length (SVL) measured with a ruler (males:
70.0 ± 0.7 mm, range = 61–79 mm; females: 72.3 ± 0.9 mm, range = 67–81 mm). Sexual maturity of lizards was estimated from their SVL based on previous studies conducted in the same area (i.e. SVL > 61 mm for males and >67 mm for females; Elvira & Vidal 1985) and only mature individuals were marked. Individuals were sexed by checking whether hemipenes were present. Males were easily assigned as either ‘green’ or ‘brown’. The coloration type was always assigned by the same observer to ensure the same criteria. Lizards were individually marked permanently by toe-clipping and with acrylic paint marks on the dorsum and released at the capture site within 5 min. These marks were only approx. 5 mm in diameter to avoid influencing the behaviour of lizards (see also Simon & Bissinger 1981).

Censuses were performed from 0800 to 1800 h GMT each day from 1 May to 30 Jun. 1998, which coincided with the mating season (Aragón et al. 2001a), to study the spatial and social relationships, spatio-temporal overlap and types of activity. Additional field work was conducted from 1 to 15 Jun. 1999 to study growth and changes in coloration of individuals studied in 1998. Finally, focal observations of lizards were performed from 1 to 17 Jun. 2000 to look for differences in time spent moving and distance travelled between lizard categories and to examine within-day variation. Field work was performed every day except when rainy or cloudy conditions precluded the activity of lizards (sunny days in 1998: 46; 1999: 11; 2000: 14). Before the data analyses, normality and homocedasticity were systematically checked for each variable using the Kolmogorov–Smirnov and Hartley tests, respectively. The variables of the levels of activity, time spent moving and distance travelled were transformed using the square root and logarithmic transformations. Non-parametric tests were used only when data did not meet the assumptions underlying linear models even after the appropriate transformations of variables. For the repeated measures models sphericity was not checked because all the within-subjects factors have only two levels and therefore each variance–covariance matrix is a vector (Quinn & Keough 2002). All average data are represented as untransformed means ± SE.

Spatial Relationships

To map lizard home ranges, the position of every individual captured or sighted was recorded on a mapped grid overlaying the study site, which corresponded to an x–y coordinate system. To maximize the independence of data points, considering movement rates of this species, the time interval between recordings of an individual was at least 1 h (Aragón et al. 2001a; see Stone & Baird 2002). Home range for each lizard was defined by the convex polygon of the area enclosed by their observation points (Christian & Waldschmidt 1984), which is widely used as a suitable method to measure home range size of lizards (Rose 1982). A band of equal width (100 m) around the study plot was included in the censuses to obtain home range information of those individuals with part of their home range outside of the plot, thus reducing a bias because of the edge effects. We used the computer program RANGES v (R. Kenward, Institute of Terrestrial
Ecology, Wareham, UK) (Larkin & Halkin 1994) to determine home range size and degree of overlap among individuals. A previous study of the same population showed that approximately 10 sightings for males and six for females described 80% of the home range estimated with all the sightings, and this was considered the minimum number of sightings to adequately represent home range size in this population (Martin & Salvador 1997; see Rose 1982; Stone & Baird 2002 for estimation procedures). Thus, in this paper, only home range data that fulfilled these requirements were used (number of sightings, males: $\bar{x} \pm 1$ SE = 13.2 ± 1.9, range = 10–54, n = 28; females: 7.5 ± 1.1, range = 6–28, n = 24).

To decide the percentage of sightings that best defined core areas of home ranges, we examined the utilization plots (Ford & Krumme 1979). These plots showed the mean and standard error of the home range size as a function of a percentage of sightings that excluded the other sightings further from the centre of the home range. The home range centres were determined with the kernel fix estimator included in the RANGES V computer program, the equivalent of the Gaussian Kernel estimator (Worton 1989) and is more robust than the simple arithmetic mean. Thus, the variance in home range size tends to a minimum at the percentage of sightings that excludes most of the excursive activity. On the other hand, the slope discontinuity of the plot is an indicator of how many sightings constitutes the core area, becoming shallower when only the core sightings remain (Kenward & Hodder 1996). The results showed that variances in home range size at 10% intervals were significantly heterogeneous in males (Hartley’s $F_{\text{max}}$ test; Quinn & Keough 2002): $F_{\text{max}} = 13057.06$, p < 0.0001) and females ($F_{\text{max}} = 12967.13$, p < 0.0001). The utilization plots of males and females showed that the variance in range become substantially smaller the 60% of sightings (Fig. 1), and

![Utilisation plot of male (above) and female (below) Lacerta monticola showing the mean and standard error of the home range size as a function of a percentage of sightings that exclude the other sightings further from the centre of the area](image-url)

Fig. 1: Utilisation plot of male (above) and female (below) Lacerta monticola showing the mean and standard error of the home range size as a function of a percentage of sightings that exclude the other sightings further from the centre of the area
were significantly smaller when compared with the total home range area (males: \( F_{\text{max}} = 81.22, \ p < 0.0001 \); females: \( F_{\text{max}} = 38.95, \ p < 0.0001 \)). Besides, the slopes of the plots in both sexes became shallower at the 60% of sightings. Therefore, taking into account also the number of fixes to obtain a representative use of the area, the core area of lizards was operationally defined at the 60% of sightings for subsequent analysis.

The degree of spatial overlap between individuals was calculated as the percentage of home range area or core area of each individual overlapped by each of his neighbours. We then calculated for each male the mean percentage of overlap by all their neighbours. To examine whether the degree of overlap with same-sex neighbours varied between green and brown males, we performed one-way ANCOVA’s (Sokal & Rohlf 1995), comparing the differences between the mean percentage of overlap on the areas (home range and core area) owned by each green or brown male. We included the SVL of males as a covariate to segregate the effects of body size and coloration. Examining the possible differences between age-related colour phases independently of size may be important because (1) within the range size obtained from the marked males in the field, 50% of body size classes are represented in both types of coloration (Fig. 2) and (2) 93.5% of all the agonistic interactions began at a relatively long distance between opponents (chases), where coloration is more likely to act as a signal, whereas only a few interactions implied physical contact (i.e. fights) (see Results).

To estimate access to potential mates, repeated measures one-way ANOVAs were used to assess variation in the mean percentage of each female’s home range overlapped by green and brown males, or the number of green and brown males that overlapped each female’s home range (Sokal & Rohlf 1995). Exclusiveness of each individual core area compared with its total area was examined comparing

![Fig. 2: Body size (snout-to-vent length) frequency distribution of brown and green males Lacerta monticola captured](image-url)
the mean percentage of area overlapped by same sex individuals on the core area with that on the total area (i.e. two measurements of overlap for each individual in a repeated measures analyses). Data analyses were performed using one-way repeated measures ANCOVAs including SVL as a covariate. We predicted that green males would have more exclusive core areas than brown males or females.

A lower density of sightings outside the core areas indicates a lower use of that space, thus denoting an excursive activity further from the home range centre. In addition, the slope discontinuity of the utilization plot may corroborate this result. Thus, to examine the excursive activity of lizards, we compared the density of sightings inside the core area (number of sightings/core area size) with the density in the border area of the home range [(total sightings−core sightings)/(total home range size−core area size)]. Differences between the density of sightings in the border and core area of each individual were analysed with Wilcoxon matched pairs test, and differences between males and females in the density of sightings in the border area were analysed with Mann–Whitney U-tests (Siegel & Castellan 1988).

**Spatio-Temporal Overlap and Types of Activity**

One of the biggest problems of field studies of activity is the confounding effect of detectability. It is very difficult to determine which individuals are active when the species is highly mobile, as in lacertid lizards (Martín & Salvador 1995). A solution to this problem is to examine the types of activity of each lizard as a function of the degree of risk, such as predation, agonistic interactions or exposure to high temperature, rather than imagine that a lizard is inactive when it is not seen. Thus, when possible the type of activity was also recorded. Activity observations were included in different categories. Conspicuous activities (CA) were those that lizards performed by moving (walking, mating, chasing, or foraging) over open areas such as rocks, grass or on shrubs and non-conspicuous activities (NCA) were those that lizards performed under cover, mainly shrubs (resting or moving slowly). Other types of activity were also recorded but not included in the CA or NCA because of the difficulty to assess their conspicuousness (for example, basking in open areas but remaining motionless).

A repeated measures two-way ANOVA (Sokal & Rohlf 1995) was used to compare the differences between the activity levels (i.e. number of observations) of green and brown males (between-subjects factor), and the differences between CA and NCA activity levels of each individual male (within-subjects factor). Differences between male categories in the types of activity were assessed a posteriori using Tukey’s honest significant difference (HSD) tests (Sokal & Rohlf 1995). Only observations clearly detected as CA or NCA were included in the analysis. We predicted that green males would spend more time involved in CA, which are more costly, than brown males.

To test for different temporal patterns of space use through the day, the area size, mean percentage of area overlapped by neighbours of the same and opposite sex, and the number of lizards that overlapped were calculated separately using
data from two daily periods: morning (between 0800 and 1300 h GMT) and afternoon (between 1300 and 1800 h GMT). The same sampling effort was carried out in both periods. Differences in variables between the two daily periods were analysed with Wilcoxon matched pairs test.

**Time Spent Moving and Distance Traveled**

During early Jun. 2000, focal observations of green and brown males and of females were performed within the study area, but outside of the study plot. Lizards found in random transects were followed. Given the large size of the area surveyed (more than 5 km²), the high lizard density (510 adult lizards/ha; based on capture/recapture estimations; unpubl. data), and because we avoided walking routes taken previously, the probability of repeated sampling of the same individuals was very low. Therefore, all measurements were treated as independent. Each lizard was followed for 5 min from 5-m distance to avoid disturbing them and binoculars were used when necessary. The time spent moving and the total distance travelled were scored for each lizard. The observations were aborted when a lizard was more than 30 s out of sight or its behaviour was influenced by the observer. Mature green and brown males and females were easily identifiable, but lizards were captured when possible to confirm the sex and measure their SVL. The sex and sexual maturity of all lizards that were captured coincided with that previously noted before capturing. Data were collected in two periods: morning (from 0900 to 1100 h GMT) and afternoon (from 1500 to 1700 h GMT) to examine within-day variation. Two-way ANOVA's (Sokal & Rohlf 1995) were performed to look for differences in time spent moving or distance travelled among green and brown males and females and between periods. Pairwise comparisons were planned using Tukey’s HSD for unequal n-tests.

**Social Relationships**

While we performed the transects in the study plot, we also recorded the agonistic interactions between males (chases and fights) observed, and when possible identified the two individuals involved. Chases involved one male (assigned ‘winner’) rapidly running toward his opponent causing, in all observations, the other individual (assigned ‘loser’) to retreat or run away without physical contact. Attacks with escalated physical combat and bites (fights) were rarely recorded. The total number of agonistic interactions and the number of interactions won and lost by green and brown males were compared with an expected binomial distribution.

Intersexual interactions were defined as the male–female interactions where males approached females slowly and began to flick on the tail or the surrounding substrate. Typically, males then gripped and shook the female’s tail near the cloaca with a gentle bite, and if the female was receptive she allowed copulation. To compare the number of interactions with females by green and brown males, we used a two-tailed binomial test (Siegel & Castellan 1988). We also noted when males...
were found close to females and followed female movements closely (within less than 0.1 m apart and during more than 5 min), which was operationally defined as a mate guarding (e.g. Olsson & Shine 1998). Binomial tests were performed taking into account the frequencies of male categories observed in the field.

Results

General Results

The sex ratio of lizards found in the study plot did not differ from 1:1 (58 males vs. 44 females; \( \chi^2 = 1.92, p = 0.16 \)). Neither were there differences in the ratio of male categories (30 green vs. 28 brown; \( \chi^2 = 0.06, p = 0.79 \)), not even when only resident males were considered (16 green vs. 12 brown; \( \chi^2 = 0.57, p = 0.44 \)).

Although the body size ranges of the two types of males overlapped (Fig. 2), green males were significantly larger (\( \bar{x} \pm 1 \text{ SE} = 73 \pm 1 \text{ mm}, \) range = 67–78 mm; \( n = 30 \)) than brown males (67 ± 1 mm, range = 61–79, \( n = 28 \); one-way ANOVA, \( F_{1,56} = 29.67, p < 0.0001 \)). In 1999, we recaptured 14 of the 28 resident males marked in 1998. All of these individuals that were categorized as green males in 1998 had grown but remained green in 1999, and all individuals categorized as brown males in 1998 had grown and turned their body coloration to green in 1999. Brown males captured in 1999 were all new small individuals that had not been previously marked in the study plot in 1998, suggesting that these newly mature males came from the 1998 non-mature class.

Spatial Relationships

There was no significant correlation between SVL and home range area in either females (Spearman rank correlation, \( r_s = 0.18, n = 24, p = 0.39 \)) or males (\( r_s = 0.32, n = 28, p = 0.41 \)). This result was similar in green (\( r_s = 0.14, n = 16, p = 0.58 \)) and in brown males (\( r_s = -0.01, n = 12, p = 0.98 \)). Although the mean home range area of all males pooled was significantly larger than that of females (Table 1; Mann–Whitney U-tests, \( Z = 3.80, p < 0.001 \)), there were no significant differences between the home range size of green and brown males (Table 1; \( Z = 0.88, p = 0.37 \)). Similarly, male core areas (all males pooled) were significantly larger than those of females (Table 1; \( Z = 3.59, p < 0.001 \)), but there was not a significant difference between the size of core areas of green and brown males (Table 1; \( Z = 0.27, p = 0.78 \)).

The mean of the average percentages of spatial overlap by all neighbour males was significantly higher on home range areas of brown males than on those of green males, even after excluding the effect of males’ body size (Table 1; one-way ANCOVA, \( F_{1,25} = 4.45, p < 0.05 \)). Similarly, the degree of spatial overlap by other males was significantly higher on the core areas owned by brown males than on those owned by green males (Table 1; one-way ANCOVA: \( F_{1,25} = 5.33, p = 0.029 \)).
The percentage of the female’s home range overlapped by green males was significantly higher than that overlapped by brown males (53.4 ± 4.8% vs. 41.7 ± 5.6%; one-way repeated measures ANOVA, $F_{1,23} = 6.95$, $p = 0.014$). Moreover, significantly more green than brown males’ areas overlapped each female’s home range (5.9 ± 0.5 vs. 4.2 ± 0.4; one-way repeated measures ANOVA, $F_{1,23} = 8.34$, $p = 0.008$).

There was a significant correlation between the mean percentage of the male’s home range overlapped by neighbour females and by neighbour males (Pearson’s correlation, $r = 0.50$, $F_{1,23} = 7.74$, $p = 0.01$), and, similarly, between the number of overlapping males and females ($r = 0.77$, $F_{1,23} = 33.14$, $p < 0.0001$). Thus, the higher the number of female neighbours the higher the number of male neighbours. There was no significant correlation between the mean percentage of the female’s home range overlapped by neighbour males and by neighbour females ($r = -0.27$, $F_{1,19} = 1.45$, $p = 0.24$), whereas the correlation between the number of overlapping males and females was significant ($r = 0.45$, $F_{1,19} = 4.76$, $p = 0.04$).

With respect to area exclusivity, the mean percentage of green male’s total home range overlapped by all neighbour males was significantly higher than that of the green male’s core area overlapped, even after excluding the effect of males’ body size (Table 1; one-way repeated measures ANCOVA, $F_{1,14} = 6.50$, $p = 0.023$) whereas there was no significant difference in brown males (one-way repeated measures ANCOVA, $F_{1,10} = 2.42$, $p = 0.15$). There was no significant difference in the degree of overlap between females when comparing the overlap on their entire home ranges with their corresponding core areas (one-way repeated measures ANCOVA, $F_{1,22} = 0.77$, $p = 0.38$).

In males, the density of sightings was significantly higher in the core area ($1.1 ± 0.3$ sightings/m$^2$) than in the border area ($0.1 ± 0.3$ sightings/m$^2$; Wilcoxon matched paired test, $Z = 4.6$, $p < 0.0001$). This result was similar in females ($2.9 ± 0.7$ vs. $0.2 ± 0.1$ sightings/m$^2$; $Z = 4.28$, $p < 0.0001$). The density of sightings in the border area was significantly greater in females than in males (Mann–Whitney U-test, $Z = 2.14$, $p = 0.03$). Supporting this result, the slope of the utilization plot was more abrupt when including the border areas in males than in females (Fig. 1). As indicated by Kenward & Hodder (1996), when

<table>
<thead>
<tr>
<th></th>
<th>Females (n = 24)</th>
<th>All males (n = 28)</th>
<th>Green males (n = 16)</th>
<th>Brown males (n = 12)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Home range size (m$^2$)</td>
<td>28.3 ± 4.9</td>
<td>134.7 ± 28.6</td>
<td>168.6 ± 46.6</td>
<td>89.6 ± 20.0</td>
</tr>
<tr>
<td>Core area size (m$^2$)</td>
<td>4.3 ± 1.9</td>
<td>17.9 ± 3.1</td>
<td>16.3 ± 3.7</td>
<td>20.0 ± 5.4</td>
</tr>
<tr>
<td>Overlap on home range (%)</td>
<td>18.2 ± 2.3</td>
<td>35.2 ± 2.7</td>
<td>28.6 ± 2.2</td>
<td>44.1 ± 4.5</td>
</tr>
<tr>
<td>Overlap on core area (%)</td>
<td>15.1 ± 4.5</td>
<td>24.6 ± 3.6</td>
<td>18.1 ± 3.3</td>
<td>33.3 ± 6.7</td>
</tr>
</tbody>
</table>

Table 1: Home range (100% of sightings) and core area size ($\bar{x} ± 1$ SE) (including only the 60% of the nearest sightings to the centre), and the percentage ($\bar{x} ± 1$ SE) of the home ranges and core areas (of females, all males pooled, and green and brown males) overlapped by same-sex neighbours of _Lacerta monticola_.

The percentage of the female’s home range overlapped by green males was significantly higher than that overlapped by brown males ($53.4 ± 4.8\%$ vs. $41.7 ± 5.6\%$; one-way repeated measures ANOVA, $F_{1,23} = 6.95$, $p = 0.014$). Moreover, significantly more green than brown males’ areas overlapped each female’s home range ($5.9 ± 0.5$ vs. $4.2 ± 0.4$; one-way repeated measures ANOVA, $F_{1,23} = 8.34$, $p = 0.008$).
Spatio-Temporal Overlap and Types of Activity

Green males showed significantly higher levels of activity than brown males (Fig. 3; two-way repeated measures ANOVA, between-subjects factor: $F_{1,36} = 5.12$, $p = 0.03$). All males pooled showed significantly higher levels of CA than of NCA (within-subjects factor: $F_{1,36} = 8.18$, $p = 0.007$), and the interaction was significant ($F_{1,36} = 5.09$, $p = 0.03$). Thus, CA levels of green males were significantly higher than those of brown males (Tukey’s HSD test, $p < 0.0001$) but there were no significant differences between the NCA of both male categories ($p = 0.58$). Additionally, the CA levels were significantly higher than NCA levels in green males ($p < 0.005$), but were not significantly different in brown males ($p = 0.97$). In contrast, the CA levels of females were significantly lower than their NCA levels (Fig. 3; repeated measures one-way ANOVA, $F_{1,31} = 5.00$, $p = 0.03$).

The area of the home range used by green males was significantly greater in the morning than in the afternoon period (Table 2; Wilcoxon matched pairs test, $Z = 1.98$, $p < 0.05$), but there was no significant difference in brown males ($Z = 0.66$, $p = 0.50$) or in females ($Z = 0.74$, $p = 0.45$). The mean percentage of the green male’s area overlapped by all neighbour males was significantly higher in the morning than in the afternoon period (Table 2; Wilcoxon matched pairs test, $Z = 2.66$, $p = 0.007$), but there was neither significant difference between periods in brown males ($Z = 0.15$, $p = 0.87$) nor in the percentage of the female’s area.

Fig. 3: Mean rate ($\pm 1$ SE) of conspicuous (CA, white) and non-conspicuous (NCA, black) activities (observations/h) of green and brown males and female *Lacerta monticola* during May and Jun.
overlapped by neighbours females ($Z = 0.92, p = 0.35$). Similarly, the number of males that overlapped with the areas used by green males was significantly higher in the morning than in the afternoon period (Table 2; Wilcoxon matched pairs test, $Z = 2.07, p = 0.038$), but there was neither significant difference in brown males ($Z = 0.61, p = 0.54$) nor in the number of females that overlapped with each female’s area (Table 2; $Z = 0.51, p = 0.95$).

The mean percentage of the green male’s home range overlapped by all neighbour females tended to be higher, although it did not reach significance, in the morning than in the afternoon period ($15.9 \pm 6.4\%$ vs. $8.1 \pm 2.2\%$; Wilcoxon matched pairs test, $Z = 1.41, p = 0.15$), whereas in brown males there was no significant difference between periods ($8.6 \pm 19.9\%$ vs. $10.3 \pm 3.2\%$; $Z = 0.05, p = 0.95$). Similarly, the number of females overlapped by green males was higher in the morning than in the afternoon period ($6.0 \pm 1.4$ vs. $2.9 \pm 0.7$ females; $Z = 1.95, p = 0.05$), whereas in brown males there was no significant difference between periods ($4.8 \pm 1.2$ vs. $3.7 \pm 1.1$ females; $Z = 0.59, p = 0.55$).

### Table 2: Area of the home range used, percentage ($\bar{x} \pm 1$ SE) of the areas of females and green and brown males overlapped by same-sex neighbours of *Lacerta monticola*, and number of neighbours of the same sex ($\bar{x} \pm 1$ SE) in the morning and afternoon periods

<table>
<thead>
<tr>
<th></th>
<th>Females (n = 24)</th>
<th>Green males (n = 16)</th>
<th>Brown males (n = 12)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area of the home range used (m²)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morning</td>
<td>12.6 ± 3.9</td>
<td>104.3 ± 31.7</td>
<td>60.0 ± 22.2</td>
</tr>
<tr>
<td>Afternoon</td>
<td>10.5 ± 3.5</td>
<td>59.9 ± 21.4</td>
<td>44.6 ± 16.9</td>
</tr>
<tr>
<td>Overlap on area used (%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morning</td>
<td>23.2 ± 7.0</td>
<td>38.3 ± 6.9</td>
<td>43.0 ± 8.3</td>
</tr>
<tr>
<td>Afternoon</td>
<td>35.2 ± 7.3</td>
<td>15.6 ± 3.0</td>
<td>37.8 ± 8.3</td>
</tr>
<tr>
<td>No. of neighbours of the same sex</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morning</td>
<td>2.5 ± 0.4</td>
<td>10.5 ± 1.7</td>
<td>8.7 ± 1.4</td>
</tr>
<tr>
<td>Afternoon</td>
<td>2.7 ± 0.5</td>
<td>7.3 ± 1.3</td>
<td>7.3 ± 1.2</td>
</tr>
</tbody>
</table>

**Time Spent Moving and Distance Travelled**

The time spent moving differed significantly between brown, green males and females (Fig. 4; Two-way ANOVA, $F_{2,117} = 45.69, p < 0.0001$), there was a significant difference between the morning and afternoon period ($F_{1,117} = 46.00, p < 0.0001$), and the interaction was significant ($F_{2,117} = 24.03, p < 0.0001$). Thus, in the morning, green males (n = 23) spent significantly more time moving than brown males (n = 20) and than females (n = 20) (Tukey’s HSD for unequal n-test, $p < 0.0001$ in all cases). By contrast, there were no significant differences in the afternoon (Green males: n = 19; Brown males: n = 19; Females: n = 21; p > 0.1 in all cases). Green males spent significantly more time moving in the morning than in the afternoon ($p < 0.0001$), but there were no significant differences in brown males and females ($p > 0.98$ in both cases). All these
influences on time spent moving were also found for the distance travelled by the lizards.

**Social Relationships**

Significantly more green than brown males were observed interacting agonistically with other males in the field (37 green vs. 21 brown; two-tailed binomial test, \( p < 0.05 \)). On 11 occasions (37.9%), the two males that participated in the agonistic interaction were both green, on 15 occasions (51.7%), one was green and one brown, and only in three interactions (10.3%), both males were brown. In the green–brown male encounters, significantly more green than brown males won the interaction (12 green vs. three brown; two-tailed binomial test, \( p = 0.035 \)).

More green than brown males were observed attempting copulations with females, although the difference did not reach significance (12 green vs. four brown; two-tailed binomial test, \( p = 0.051 \)). However, the results suggested that green and brown males might not be equally successful at obtaining matings because of the successful copulations observed (those with hemipenial intromission and with a long enough duration that presumably allowed male ejaculation), five were performed by green males and only one was performed by a brown male. This difference was, however, not significant (two-tailed binomial test, \( p = 0.12 \)). On the other hand, green males performed a significantly higher number of mate guardings than brown males (16 green vs. four brown; two-tailed binomial test, \( p = 0.008 \)).
Discussion

Taken together, the difference in body size between the two categories of males and the change of coloration between years indicate that male *L. monticola* present two phases of coloration during their ontogeny. In several lizard species colour polymorphism is associated with alternative reproductive strategies of males of similar age (e.g. Sinervo & Lively 1996; Zamudio & Sinervo 2003). A recent study reflects the ontogeny of territoriality as it relates to body size and throat colour in *Uta stansburiana*, an iguanid lizard species that matures in 1 yr and dies after only a single reproductive season and male colour morphs are genetically fixed (Calsbeek & Sinervo 2002). In contrast, colour phases in *L. monticola* are ontogenetically plastic. Brown males are younger males of recent sexual maturity that will adopt a permanent green coloration in the following breeding periods. Both brown and green males are sexually mature and compete for access to females, but the results indicate that competitive ability of brown males in intrasexual interactions is lower. This leads to different tactics in the use of time and space that may favour intraspecific resource partitioning in this lizard.

Spatial Overlap and Area Defence

After controlling for size, green males had more exclusive areas than brown males. The core areas of green males were more exclusive than their entire home ranges, whereas this difference was not found in brown males or in females. These results suggest that green males compete for resources (e.g. food, shelters, mates) by excluding potential competitors from their most used area (where the density of sightings is higher). The degree of overlap being lower in the area where activity is high, the probability of access to resources must be higher. The degree of overlap with female home ranges was higher in green than in brown males, and more green than brown males overlapped the female home ranges. Female lizards generally mate with the male whose territory overlaps theirs (Stamps 1983), and it is very likely that the males that overlap with females more extensively also have greater opportunities to mate. In fact, a previous study with the lizard *Sceloporus virgatus* showed a strong correspondence between male–female spatial proximity and actual paternity estimated by fingerprinting (Abell 1997).

Spatio-Temporal Overlap and Activity

Comparing the types of activities within each individual lizard, we found that green males spent more time in CA than NCA, and more time in CA than that of brown males. The benefits of higher levels of CA to green males may be territorial defence, maintenance of social status and increasing access to potential mates. Because female *L. monticola* have limited movement rates, spending long periods stationary, and use a less active foraging strategy (Martín
green males might travel from one female’s activity centre to another, as suggested for male *Sceloporus virgatus* (Rose 1981). High quality males that are able to spend more time in CA, might also be more efficient in other activities such as avoiding predators (Martín & López 2000). The costs of CA activities may be higher for brown males than for green males, as they also have to use energy in growth, being younger (Olsson 1994b). Furthermore, lower CA levels may be advantageous for brown males because it would reduce the cost of agonistic encounters (Cooper & Vitt 1987), the risk of predation (Magnhagen 1991) and the costs of maintenance at higher activity temperatures (Rose 1981). Thus, brown males may increase the probability of surviving to mate in the next breeding seasons when they become higher status males.

Interestingly, in females the NCA levels are higher than the CA levels. This may allow females to invest more energy in egg development and somatic growth, which is correlated with clutch size (e.g. Lister & Aguayo 1992), and reduce the risk of being detected by predators. Besides, as green males invest more time and energy on moving in open areas this may allow them to travel between shrubs, where females remain relatively stationary.

Our results show that the benefits of greater overlap with females in terms of mating success (Stamps 1983; Abell 1997) are accompanied by the cost of an increasing overlap with competitor males. This cost may be reduced on smaller brown males by spending less time moving and by travelling shorter distances than green males. The consequent cost of reduced access to mates may be low as females seem to reject copulation attempts by smaller brown males (Martín & Salvador 1993, López et al. 2003; see also Cooper & Vitt 1987, Martín & Forsman 1999 for other lizards).

Although green males are able to withstand the costs of agonistic interactions, this also implies costs in terms of time, energy and risk of predation. Therefore, an intermediate alternative tactic to reduce the costs but not the benefits should be advantageous. For green males the area used, and the overlap with other males, was greater in the morning than in the afternoon. In contrast, we did not find such differences between the morning and afternoon periods in brown males or in females. Similarly, most activity of adult *Sceloporus jarrovi* occurs in the early morning while most juvenile activity occurs around noon (Simon & Middendorf 1976). A higher activity in the morning may allow green males to bask, feed and mate in a shorter period of time because they have priority to the resources in relation to brown males, and then, they may reduce their activity in the afternoon. In contrast, brown males might have to disperse their activity during other periods of the day. A previous study suggested that subordinate male *L. monticola* could use alternative mating tactics (Martín & López 2000) as it has been proposed in other lizards (Olsson 1994a; Baird et al. 1996; Baird & Timanus 1998; Martín & Forsman 1999, Zamudio & Sinervo 2003) and birds (Lyon & Montgomerie 1986). Thus, brown males could try to perform sneak matings with the nearest females when green males decrease activity (Cooper & Vitt 1987; Martín & Salvador 1993).
Social Interactions

Only two fights with physical combat were observed; most of the interactions consisted of chases without physical contact. Previous studies have shown that costly interactions such as fights occur when the competitive ability of the two opponents is similar (Maynard-Smith 1982; Huntingford & Turner 1987; Stamps & Krishnan 1994a). A field study with *Anolis aeneus* demonstrated that dyads that fought in the settlement period established mutually non-overlapping home ranges (Stamps & Krishnan 1997) and rarely engaged in further interactions, whereas those that began with a chase engaged in many subsequent interactions (Stamps & Krishnan 1998). In territorial systems and dominance hierarchies, individual recognition may help to reduce the intensity and frequency of agonistic encounters. In fact, a previous study suggested that male *L. monticola* are able to discriminate among individual neighbours and non-neighbours using chemical cues (Aragón et al. 2001b). Observations come from a natural population where the spatial and social relationships were already established and presumably stable. Therefore, frequent fights between neighbour males should be both unnecessary and potentially costly.

Green males were more successful in intrasexual interactions than brown males. This may affect male spatial relationships. Other studies with lizards showed that encounters with a clear winner and loser established dominant–subordinate relationships that were rarely reversed later (Stamps & Krishnan 1994b). Besides, more green than brown males participated in agonistic interactions. Thus, chases may function to maintain a high social status and an exclusive area.

This study demonstrates that green males have a higher competitive ability than brown males. If bright coloration reliably signals fighting ability, it should be costly as demonstrated in other lacertids (Olsson 1994a,b; Martin & Forsman 1999; see Whiting et al. 2003). Larger male *Lacerta agilis* present a bigger area of bright green coloration on their body sides than smaller recently matured males, which invest less energy in producing this type of pigment and on engaging in costly interactions. It may be too costly for small males to invest the same amount of energy and nutrients in coloration and agonistic interactions as larger males as they also distribute the energy to somatic growth (Olsson 1994b). Brown male *L. monticola* are smaller and participate in less potentially costly interactions, therefore, a similar situation might occur in this species, preventing smaller recently mature males from developing dishonest signals.

The fact that there are agonistic interactions between green and brown males indicates competition for access to resources. Most of these interactions were initiated by the green male that chased the brown male. Moreover, the number of green males that were seen interacting with a female was higher, although not significantly so, than the number of brown males. Alternatively brown males may perform their copulations less conspicuously than green males. Besides, more green than brown males were observed guarding females.

In conclusion, this study demonstrated that social and spatial relationships differ between the two ontogenetic colour phases of male *L. monticola*. Green
males have higher social status than brown males, which may allow them greater access to females, and different spatio-temporal tactics. Dominant green males may optimise their activity tactic to maximize mating success, whereas brown males may reduce the costs of agonistic encounters by performing less conspicuous activities. These behavioural differences between males show plasticity through ontogeny. Brown males acquire higher social status when they become older and green in further breeding seasons. The existence of alternative tactics may reduce intraspecific competition and help to stabilize the social system of this lizard.

Acknowledgements

We thank J. Lazarus and two anonymous reviewers for helpful comments, and ‘El Ventorrillo’ MNCN Field Station for the use of their facilities. Lizards were captured under the license from the ‘Consejerı´a del Medio Ambiente de la Comunidad de Madrid’ (Spain). Financial support was provided by the MCYT projects BOS 2002-00598 and BOS 2002-00547.

Literature Cited


Received: April 27, 2004

Initial acceptance: August 28, 2004

Final acceptance: September 9, 2004 (J. Lazarus)