Interpopulation Home Range Comparison of a Temperate Lizard

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ABSTRACT: Home range size was studied in three populations of Lacerta vivipara at Mont Lozère, France (1400 m). A population-environment system approach was used to detect the relative importance of several ecological factors in the determination of home range size. Differences in individual lizard sizes and masses, population densities, and physical environments among the three study sites were obtained. Diverse factors were found to affect home range size in males and females. Interactions among several factors render different effects on home range determination than if they were considered separately. Home range size was found to be closely related to the physical features of the habitat. The main habitat features that define home range size were structural microhabitat characteristics (shrub cover, floristic richness, and average plant height). Prey abundance and population density also had an important role in determining home range size. Future work should consider a system approach in order to clarify the impact of multiple factors on home range determination.

INTRODUCTION

Home range size is often assumed to be a function of different individual characteristics, such as body size (Turner, et al., 1969; Christian and Waldschmidt, 1984), sex (Ruby, 1978; Smith, 1985), age and experience (Davis and Ford, 1983), social status (Jones and Droge, 1980), and sexual activity (Rose, 1982; Stamps, 1983). Home range size is also influenced by several population attributes like density (Morse, 1976; Rose, 1982), social interactions (Stamps, 1977; Schoener and Schoener, 1982) as well as intra- and interspecific competition (Douglas, 1976; Trombulak, 1985). Different habitat features may also play an important role in defining home range size, for example climatic changes (Christian, et al., 1983), prey abundance, distribution and renewal (Simon, 1975; Iverson, 1979; Ebersole, 1980; Erikstad, 1985; Polis, et al., 1985), habitat productivity (Harestad and Bunell, 1979), type and habitat quality (Franzblau and Collins, 1980), and burrows and refuges from predators (Covich, 1976; Orians and Pearson, 1979).

Although a great deal of research has been devoted to extensive descriptions of these factors, most of the studies take into account only one or two factors at a time. Questions such as how do several factors interact to determine home range size, or what is the relative importance of each factor in defining it, still remain unanswered. This paper describes home range size for three populations of Lacerta vivipara located in neighboring sites. Individual characteristics, population features, and environmental patterns were examined and related to home range size.

This work was formulated within the general framework of the study of dynamics and demographic strategies of the European common lizard populations (Pilorge, 1981, 1982, in press; Pilorge, et al., 1983).

MATERIALS AND METHODS

Lizards are excellent subjects for the study of home range, because individuals can be easily observed, captured and marked (Tinkle, 1967; Simon, 1975; Ortega, 1986). Lacerta vivipara is a small lizard (40-75 mm SVL at sexual maturity) with an extremely broad distribution in Europe.
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FIG. 1. Geographic situation of the three populations examined in this study.

FIG. 2. Accumulative home range size for several average lizards from the CMB population.
and Asia: from Finistere to the Far East (Siberia, North China and Japan), and from the Pyrenees to North Cape (Pilorge, 1981). This viviparous lizard also has a wide altitudinal distribution. Three *L. vivipara* populations were studied in the mountainous regions of the province of Mont Lozère, France (Fig. 1). Information about climate and vegetation of the three study sites can be found elsewhere (Pilorge, in press). Each study site comprises an area of 2500 m$^2$. The first site, located at the Mas de la Barque (CMB), is delimited by natural boundaries (a forest, a brook and prairies) which are seldom visited by the lizards. The Chalet du Mont Lozère study site (CCML) is also delimited by a forest and a prairie, where lizards are rarely found. The last site is located at the Plateau de La Croix de L'Ermite (CPCE). Although this area is not truly discontinuous from the surrounding area, it can still be easily delimited from the general area because it represents a physiognomic unit.

During June, 1985, the following habitat features were studied: exposure, with a compass; slope, with a clinometer; soil depth, evaluated by making holes in the ground; soil humidity, roughly estimated by examining aspect and consistency of the soil in relation to its relative moisture. Structural vegetation features such as plant cover and mean height were also recorded in each study site by making modified Canfield lines (Buell and Cantlon, 1950). Relative abundance of consumed prey by lizards in each site was evaluated using an entomological net. Net contents, after 20 net strokes over vegetation, were placed into plastic bags containing cotton saturated with ethyl acetate. Afterwards, all the insects were fixed in vials with 70% alcohol. Net strokes were accomplished 10:30 hrs., 12:00 hrs., 14:00 hrs., 16:00 hrs., and 17:30 hrs. for six days in each site. Insects were identified to Order level, counted, and measured with a stereoscopic microscope provided with an ocular micrometer. Sex, snout-vent length, and body mass of individual lizards were recorded from each study population. Density was estimated by a multiple recapture technique (Schumacher-Eschemeyer index; Pilorge, 1981).

In each study site a permanent quadrat was established by placing 6 rows and 6 columns, fixed by stakes, 10 m apart. The position of each stake was recorded by assigning letters and numbers to rows and columns respectively. Over 513 lizards were captured in the grids of the three study sites. They were marked by toe-clipping and with color dots.

Individual color marking was accomplished by using oil paint with several dot combinations on the backs of the lizards. We carefully searched for active lizards alternatively in each study site, most of the location records being obtained by observing the lizards at a distance. Only the first sightings of each lizard per census (634) were considered in this study.

In each study site, censuses were carried out at distinct hours during a day, following a different route on each occasion. Data of lizards with less than five recapture locations or inhabiting the marginal areas of the quadrats were excluded from the analysis.

The convex polygon technique (Mohr, 1974; Stickel, 1954) was used to measure the home range area when five or more sightings were recorded. This method is a widely-used technique to estimate home range area, and it has been demonstrated to be a good estimator of the area used by the lizards as related to other methods (Gutiérrez and Ortega, 1985). Nevertheless, a small number of recapture points can severely bias home range estimates (Jorgensen and Tanner, 1963; Ortega and Gutiérrez, 1985). For this reason we used a modified convex polygon technique for small sample sizes proposed by Rose (1981), which is a modified version of the one introduced by Jenrich and Turner (1969).

Thus, we first determined the minimum number of sightings above which the home range size did not increase. The estimated home range for the CMB population was asymptotic when 10 sightings per individual (for males and females) were recorded (fig. 2). For the CCML and CPCE populations, asymptotic values were reached at 14 and 12 sightings.
**TABLE 1.** Average snout-vent length, mass, and home range size for individuals of the studied populations (standard deviations are indicated in parentheses; \( N \) is sample size).

<table>
<thead>
<tr>
<th>Populations</th>
<th>Sex</th>
<th>Snout-vent Length (mm)</th>
<th>Body Mass (gr)</th>
<th>Home Range Size (m²)</th>
<th>( N )</th>
</tr>
</thead>
<tbody>
<tr>
<td>CMB</td>
<td>F</td>
<td>55.1 (3.9)</td>
<td>3.7 (0.9)</td>
<td>563.9 (220.3)</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>51.5 (3.9)</td>
<td>3.1 (0.6)</td>
<td>584.2 (58.1)</td>
<td>8</td>
</tr>
<tr>
<td>CCML</td>
<td>F</td>
<td>57.0 (3.2)</td>
<td>3.5 (0.5)</td>
<td>1059.9 (735.4)</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>51.3 (2.7)</td>
<td>3.1 (0.7)</td>
<td>1692.1 (835.0)</td>
<td>18</td>
</tr>
<tr>
<td>CPCE</td>
<td>F</td>
<td>54.2 (3.5)</td>
<td>3.2 (0.7)</td>
<td>538.9 (328.3)</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>47.7 (4.2)</td>
<td>2.6 (0.5)</td>
<td>1079.7 (419.1)</td>
<td>8</td>
</tr>
</tbody>
</table>

**TABLE 2.** \( F \) values obtained by multiple comparison tests per sex for differences in SVL (a) and home range size (b). The upper part of the table shows the \( F \) values for males (df=1,31) and the lower part for females (df=1,43) and (c) \( F \) values resulting from the multiple comparison analysis performed to test differences between males and females within each population for each independent variable. Significance level: *** \( \alpha \leq 0.001; ** \( \alpha \leq 0.01; * \alpha \leq 0.05.

<table>
<thead>
<tr>
<th></th>
<th>M</th>
<th>F</th>
<th>M</th>
<th>F</th>
<th>M</th>
<th>F</th>
<th>M</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>CMB</td>
<td>----</td>
<td>0.25</td>
<td>5.58*</td>
<td></td>
<td>CMB</td>
<td>----</td>
<td>17.72***</td>
<td>3.38</td>
</tr>
<tr>
<td>CCML</td>
<td>2.24</td>
<td>----</td>
<td>6.87*</td>
<td>CCML</td>
<td>6.51*</td>
<td>----</td>
<td>4.38</td>
<td></td>
</tr>
<tr>
<td>CPCE</td>
<td>0.60</td>
<td>3.24</td>
<td>----</td>
<td>CPCE</td>
<td>0.06</td>
<td>7.58**</td>
<td>----</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Population variable</th>
<th>CMB</th>
<th>CCML</th>
<th>CPCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Home range size</td>
<td>1.16</td>
<td>2.10</td>
<td>13.81***</td>
</tr>
<tr>
<td>SVL</td>
<td>6.38*</td>
<td>28.57***</td>
<td>21.20***</td>
</tr>
<tr>
<td>Body mass</td>
<td>2.50</td>
<td>3.95</td>
<td>3.194</td>
</tr>
</tbody>
</table>
respectively for males, and 12 and 10 for females.

To test differences among home range size, snout-vent length and body mass, as related to study site and sex among the individuals of the three populations, two-way ANOVAs (Sokal and Rohlf, 1981) were performed. Multiple comparison tests were done subsequently to determine which individuals were significantly different in the considered variables by study site and sex.

The comparison among several populations would be of little interest if we fail to look for the ecological factors which determine the observed differences; therefore, environmental features (which are very important to these small ectothermal organisms) in the lizard habitats were also compared.

Each environmental feature measured was related to home range size through lineal correlations (Sokal and Rohlf, 1981). However, a significant correlation does not necessarily mean that a causal effect exists between each pair of variables. Also, some variables can be related significantly when considered in groups even if they are not statistically significant when considered alone. Therefore, a Principal Component Analysis (PCA; Morrison, 1981) was performed including all of the variables recorded, in order to select those that were highly correlated among them and that explained the greatest percentage of variance in the habitat and individual features measured.

Based on the results obtained from the PCA, we proceeded to combine those variables with the higher loadings for each principal component by performing a Multiple Regression Analysis (Draper and Smith, 1981) to establish the correlation and association among the combined environmental characteristics and populational features with home range size. We also performed a stepwise multiple regression analysis (Draper and Smith, 1981) entering all the measured variables as independent variables except the home range size, which was considered as the dependent variable.

RESULTS

Interpopulation Comparisons

*Lacerta vivipara* individuals from the three populations present a great variability among the different characteristics measured. Average values of SVL, mass and home range size for lizards are shown in Table 1. The results of the two-way ANOVAs analyses indicate that lizards belonging to the three local populations differed in home range size ($F = 13.17; 2, 74$ d.f.; $p < 0.001$) and SVL ($F = 5.90; 2, 74$ d.f.; $p < 0.01$) but not in body mass ($F = 2.12; 2, 74$ d.f.; $p > 0.05$). Sex differences were also significant considering home range size ($F = 5.53; 1, 74$ d.f.; $p < 0.01$), SVL ($F = 44.81; 1, 74$ d.f.; $p < 0.001$) and mass ($F = 9.18; 1, 74$ d.f.; $p < 0.01$). However, none of the interaction terms (study site by sex) were statistically significant.

The results of the multiple comparison tests performed with the factors discussed above (Table 1) revealed that there were no statistical differences in body length among females of the three populations. The contrary was true of males: the CPCE males were significantly shorter than those from the CCML and the CMB populations (Table 2a). Home range size was also different per sex and among study sites. The females from the CCML population presented the greatest home range size compared with the females from the other two populations. The same occurred with the males from CCML: CPCE and CMB males had smaller home range sizes (Table 2b).

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The multiple comparison tests concerning sex revealed that there were not significant differences in body mass between males and females of each population (Table 2c). Within populations females were larger than males; however, females' home range size was smaller than that of males, particularly in the CPCE population.

Habitat Features

The three study sites had different physical characteristics, lizard population densities, and prey abundances (Table 3). The CMB site had the most diverse structural features as well as
TABLE 3. Environmental features of the three study sites, lizard density (number of individuals ha\(^{-1}\)) and prey abundance for the lizards (average arthropod number collected by 20 strokes). From Khodadoost, et al., 1986).

<table>
<thead>
<tr>
<th>Exposure</th>
<th>CMB</th>
<th>CCML</th>
<th>CPCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope</td>
<td>2%</td>
<td>15%</td>
<td>5%</td>
</tr>
<tr>
<td>Average plant height (cm)</td>
<td>30-35</td>
<td>20-25</td>
<td>15-20</td>
</tr>
<tr>
<td>Plant cover:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small shrubs</td>
<td>80%</td>
<td>30%</td>
<td>85%</td>
</tr>
<tr>
<td>Grass</td>
<td>40%</td>
<td>80%</td>
<td>15%</td>
</tr>
<tr>
<td>Bare soil</td>
<td>0%</td>
<td>1%</td>
<td>3%</td>
</tr>
<tr>
<td>Floristic richness (species number)</td>
<td>55</td>
<td>48</td>
<td>31</td>
</tr>
<tr>
<td>Soil:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Comparative humidity</td>
<td>+++</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>60</td>
<td>60</td>
<td>60</td>
</tr>
<tr>
<td>Lizard density</td>
<td>1040</td>
<td>516</td>
<td>464</td>
</tr>
<tr>
<td>Arthropod number</td>
<td>386</td>
<td>595</td>
<td>368</td>
</tr>
</tbody>
</table>

the highest lizard density. Meanwhile, the CCML habitat harbored the highest number of arthropods and thus of potential prey for lizards. This site also showed the smallest amount of shrub cover. Finally, the CPCE habitat presented the lowest lizard density and the lowest floristic richness as well as the least mean plant height, but the highest shrub cover.

**Home Range Determination**

Significant correlations between body mass and home range were obtained (Table 4). However, body mass by itself does not explain the larger home range size of CCML females because body mass and size of the females of the three populations are statistically the same (Table 2).

Furthermore, we found that some other of the measured variables were correlated significantly with home range size, when they were considered separately: shrub cover \((r^2 = 0.28, n = 80, p<0.001)\), grass cover \((0.21, p<0.001)\), habitat exposure \((0.15, p<0.001)\), habitat slope \((0.33, p<0.001)\), prey abundance \((0.27, p<0.001)\), individual’s sex \((0.15, p<0.001)\) and population density \((0.09, p<0.01)\).

However, the stepwise multiple regression analysis shows that home range size is related to individual sex \((333.318)\) and habitat slope \((58.305)\) with an \(r^2 = 0.331\) \((F = 19.03; 2, 77\) d.f.; \(n = 80; p < 0.001)\). But because of the meaningless biological interpretation of the habitat slope, we proceeded to analyze the data by performing the PCA. The results of the Principal Component Analysis performed with all the measured variables indicate that the first three principal components explain 91% of total variance in characteristics of the three populations. The highest loadings in the first principal component (which accounted for 43.92% of the explained variance) included lizard density.
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(loading = 0.65) and several physical habitat features, such as: floristic richness (0.99), bare soil cover (0.98), soil humidity (0.92), average plant height (0.82), and grass cover (0.70). The major features comprised in the second principal component (which explained 33.84% of the total variance) were slope (-0.96), prey abundance (-0.87), small brush cover (0.87), population density (0.74), grass cover (0.70), home range size (-0.62), and mean plant height (0.55). The third principal component (which accounted for 13.31% of the total variance) included high loadings only for descriptive individual characteristics such as body size (-0.91) and body mass (-0.82), and for the sex of lizards (0.61).

This way lizard home range size was found to be appropriately defined by:

\[ HR = 6099.0 - 53.6 \text{SC} - 32.0 \text{GC} + 256.3 \text{PH} + 29.2 \text{SL} - 5.7 \text{N} - 6.1 \text{PA}. \]

\[ r^2 = 0.549, F(6,73)=5.246, n=80, p<0.001 \]

where: HR is home range size, SC is shrub cover, GC is grass cover, PH is plant height, SL is slope, N is population density, and PA is prey abundance.

DISCUSSION

Important differences among several biological and environmental features of the studied populations were found. One of these is concerned with home range size of individuals. Several authors have stated that home range size can be related to single factors such as body mass (Christian and Waldschmidt, 1984; Turner et al., 1969). However, a lizard's home range can change in many unpredictable ways beyond what body mass determines (Table 4). The results obtained for the males of the CMB population support this idea (Tables 1 and 2): males' body size and body mass are the highest, but they have the smallest home range.

The multivariate approach presented here shows that the joint effects of physical and biological factors yield a better understanding of home range size determinants. This comprehensive point of view can't be accomplished when each factor is considered separately. Home range size is the result of an interacting system which depends on several features. The multiple regression models show how home range size (as well as lizard density) are related to several environmental features. Home range size is negatively related with prey abundance, population size, shrub and grass cover. This result is expected considering that individuals who live in better habitats do not need to range over large areas to fulfill their requirements and therefore they don't need to hold large home ranges.

Lizard density is associated positively with those structural characteristics of the habitat that enhance the options for adequate thermoregulation and protection of individuals. Lizard density is negatively associated with those features that cause the loss of such opportunities, such as those sites with great portions of the area deprived of vegetation.

The highest lizard density was found at CMB, where the structural microhabitat characteristics (shrub cover and floristic richness) were more favorable, in spite of harboring low prey abundance (Table 3). This could be explained because lizards strongly depend upon microhabitat to thermoregulate and to escape from predators (Ortega et al., 1982). Boulders, small trees, and mainly low shrubs are very important to achieve these behaviors in lizards.

The closer dependence of these lizards to structural microhabitat characteristics could help explain the puzzling result of significant negative correlation between home range size and body mass in males at CCML (Table 4). This habitat has not only the smallest shrub cover, but also very few juniper bushes (Table 3). The few bushes are generally occupied by the largest males, which may be the dominant individuals. Males holding the best places only need to move short distances to thermoregulate and especially to escape from predators. Those males holding home ranges that lack such safe shelters would be forced to move.
further to fulfill their thermal requirements and to escape from predators. Therefore, they must range over larger areas. This behavior may be followed by the CCML males which have the greatest average home range size (Table 1), and whose locality has the fewest safe shelters.

Males had larger home ranges than females at CCML and at CPCE, but not at CMB (Tables 1 and 2). The high lizard density (Table 3) found at CMB may explain why home range sizes don’t differ between sexes at this site. A habitat with favorable trophic and spatial resources may allow high density. High density increases the number and frequency of interactions between individuals. As males of this species are more involved in social interactions than females (Heulin, 1985), one can expect that the size of male home ranges will be more influenced by density than those of females.

Previous studies on several taxa have shown that home range size is related to individual, population or habitat features considered separately (Waldschmidt, 1983; Smith, et al., 1984; Hulse, 1985; Polis, et al., 1985; Trombulak, 1985). However, our results suggest that several factors can interact simultaneously to determine home range size. In *Lacerta vivipara* populations, home range size seems to be a function of physical features of the habitat (mainly structural microhabitat characteristics) related to individual behavior and population density. The overall result of the interaction is also affected by food abundance. Surely much experimental work remains to be done to elucidate all the ecological determinants of home range size. However, if one wishes to achieve a comprehensive view of the ecological factors and mechanisms that determine and regulate home range size as well as the reciprocal influences of behavior and demography on one another, an holistic approach would seem necessary.

**ACKNOWLEDGEMENTS**

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**TABLE 4.** Results of regression analysis between home range size log$_{10}$ (m$^2$) and body mass log$_{10}$ (gr) of adult lizards in three populations for each sex.

<table>
<thead>
<tr>
<th>Population</th>
<th>Sex</th>
<th>Regression Model</th>
<th>r</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>CMB</td>
<td>F</td>
<td>$y = 0.85x + 2.28$</td>
<td>0.71**</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>$y = 0.58x + 2.42$</td>
<td>0.93***</td>
<td>8</td>
</tr>
<tr>
<td>CCML</td>
<td>F</td>
<td>$y = 4.62x + 0.36$</td>
<td>0.75*</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>$y = 2.41x + 4.31$</td>
<td>-0.72**</td>
<td>18</td>
</tr>
<tr>
<td>CPCE</td>
<td>F</td>
<td>$y = 1.25x + 2.00$</td>
<td>0.34</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>$y = 0.75x + 3.31$</td>
<td>-0.40</td>
<td>8</td>
</tr>
<tr>
<td>ALL</td>
<td>F</td>
<td>$y = 1.48x + 1.94$</td>
<td>0.47**</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>$y = 0.41x + 3.23$</td>
<td>-0.13</td>
<td>34</td>
</tr>
</tbody>
</table>
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LITERATURE CITED


