Seasonal changes in activity and spatial and social relationships of the Iberian rock lizard, *Lacerta monticola*

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Abstract: We conducted a field study to examine the significance of the seasonal changes in activity levels, spatial relationships, and social interactions of the Iberian rock lizard, *Lacerta monticola*, during the same favorable climatic period. Activity level, movement rate, home-range size, number of same-sex neighbors, and number of agonistic interactions decreased as the mating season finished for males but not for females. The number of females' home ranges overlapped by the home range of each male was also higher in the mating season than in the nonmating season. Measurements of available ambient temperatures showed that the thermal environment was suitable for the activity of lizards in both seasons, therefore the seasonal changes cannot be explained by thermal constraints. Males gain access to several females by increasing their home-range size, thus overlapping a larger number of females' home ranges, but as a consequence, also those of a larger number of male competitors. Thus, the cost of incurring agonistic interactions also increases. These results suggest that because activity and aggressiveness in males are related to their mating success, the balance between the costs and benefits of their activity and spatial strategies differs seasonally, and this may be the cause of the observed seasonal changes.

Résumé : Nous avons procédé à une étude sur le terrain pour examiner l'importance des changements saisonniers des niveaux d'activité, des relations spatiales et des interactions sociales chez le lézard *Lacerta monticola* au cours d'une même période climatique favorable. Le niveau d'activité, les taux de déplacement, la taille du domaine, le nombre de voisins de même sexe et les interactions agonistiques diminuent vers la fin de la saison chez les mâles, mais pas chez les femelles. Le nombre de domaines de femelles chevauchés par les domaines de chacun des mâles est plus élevé durant la saison des accouplements qu'en dehors de la saison. Les mesures disponibles de température ambiante démontrent que le milieu thermique est propice à l'activité des lézards au cours des deux saisons et, conséquemment, les changements saisonniers ne peuvent pas s'expliquer par des contraintes thermiques. Les mâles gagnent l'accès à plusieurs femelles en augmentant les dimensions de leur domaine, chevauchant ainsi un plus grand nombre de domaines de femelles, mais aussi, nécessairement, les domaines d'un plus grand nombre de mâles compétiteurs. Le coût des interactions agonistiques augmente donc aussi. Ces résultats indiquent que, parce que l'activité et l'agressivité des mâles sont reliées au succès de leurs accouplements, l'équilibre entre les coûts et les bénéfices de leur activité et leurs stratégies spatiales varient selon la saison, ce qui pourrait expliquer les changements saisonniers observés.

[Traduit par la Rédaction]

Introduction

It is widely known that the activity of lizards is related to the characteristics of the thermal environment (Schoener 1970; Porter and Tracy 1983; Labra and Rosenmann 1992). However, there is evidence that a lizard's activity does not only depend on favorable thermal conditions (Porter et al. 1973; Simon and Middendorf 1976; Rose 1981). For a lizard, to be active provides benefits such as thermoregulation, food, and mating (Huey 1982), but an active lizard may also incur costs due to an increase in predation (Magnhagen 1991) or agonistic encounters (Marler and Moore 1988; Martín and López 2000). Thus, inactivity may be adaptive, since if a lizard reduces its activity, these costs may also be reduced (Rose 1981; Martín and López 2000).

Most studies of the responses of lizards to seasonality examine the differences between the effects of favorable and unfavorable climatic periods after strong seasonal changes, i.e., in a severe climate (e.g., Fleming and Hooker 1975; Lister and Aguayo 1992; Sound and Veith 2000). On the other hand, seasonal changes in the behavior of lizards depend, at least in part, on the endogenous circadian system (Foà et al. 1994; Innocenti et al. 1994). However, seasonal changes in the behavior of lizards have often been examined as a part of studies in which this was not the general objective. Therefore, studies that have this topic as their main focus are needed. A study of species in which seasonal changes in activity and aggressiveness occur together with changes in mating behavior, and independently of climatic conditions, may contribute to understanding the adaptive significance of activity level, aggression, and territoriality.

Lacerta monticola is a small diurnal lacertid lizard found

Received January 23, 2001. Accepted September 4, 2001. Published on the NRC Research Press Web site at http://cjz.nrc.ca on November 6, 2001.

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DOI: 10.1139/cjz-79-11-1965

mainly in rocky habitats in some of the high mountains of the Iberian Peninsula. Lizards are active from May to October, mating occurs in May–June, and a single clutch is produced in July (Elvira and Vigal 1985). In this species, males are polygynous and gain access to several females by increasing their home-range size, thus overlapping a higher number of females' home ranges, but as a consequence, the number of home ranges of male competitors that are overlapped also increases. It is supposed that this situation confers a benefit in terms of mating success (Stamps 1983), but also increases the risk of incurring agonistic interactions with other males. Male lizards that are frequently engaged in agonistic interactions may incur greater energetic and survival costs derived from higher activity levels (Marler and Moore 1988). In this context, the balance between the costs and benefits of a particular home-range size should differ between the mating and nonmating seasons. Therefore, since the costs (i.e., the risk of incurring agonistic interactions) would exceed the benefits (i.e., opportunities of mating with a female) in the nonmating season, mechanisms for reducing these costs would be advantageous. The potential saving in energy is specially important in *L. monticola* because they have only a short period of activity during which to store reserves to survive a long winter.

In this study we examined seasonal changes in activity level, home-range size, spatial relationships, and social interactions of lizards of both sexes in the field during the same favorable climatic period. We predicted that if increased levels of aggression and activity in males are intended to increase their mating success, then as the mating season finishes, males should decrease their activity levels and should also tend to reduce their home-range size. In contrast, females should not change their activity level or home-range size because they need resources for the developing clutch during the nonmating season.

Methods

Spatial relationships and activity

Fieldwork was done during June–July 1998 at Alto del Telégrafo in the Guadarrama Mountains of central Spain at an elevation of 1900 m. The study site is composed of patches of large granite rocks and scree interspersed by shrubs (*Cytisus oromediterraneus* and *Juniperus communis*), together with meadows of *Festuca* sp. and other grasses (Martín and Salvador 1992). A 0.2-ha plot (50 × 40 m) was gridded into 20 quadrants of 100 m^2 each. This plot size allowed us to differentiate between residents and transients by closely monitoring the activity of lizards (Rose 1982); a larger plot would decrease the probability of sighting a particular lizard, therefore it would be more difficult to separate transients from residents.

During the study, 32 males (snout-to-vent length (SVL) = 69.8 ± 0.8 mm (mean ± SE)) and 26 females (SVL = 73.8 ± 1.3 mm) were captured by noosing and individually marked with paint on the back and remarked when necessary. Sexual maturity of lizards was estimated from their SVL and only mature individuals (SVL > 61 mm for males and SVL > 67 mm for females; Elvira and Vigal 1985) were marked. We performed censuses each day during June and July 1998 from 08:00 to 18:00 GMT, but only when climatic conditions were favorable for lizard activity. When lizards were captured or sighted we noted the date, time of the day, and their location on a *x–y* coordinate map. Censuses were also performed in a border zone of 100 m^2 to obtain information on those individuals that might have part of their home range outside of the plot. To ensure independence of data, the time interval between locations was at least 1 h. We used the computer program RANGES V (written by R. Kenward, Institute of Terrestrial Ecology, Wareham, Dorset, U.K.) (Larkin and Halkin 1994) to determine home-range size using the convex polygon method, which is suitable for measuring home-range size (Rose 1982). Lizards with less than three sightings on different days were considered transients.

Data were divided into five consecutive periods of 7 consecutive days during which lizards were active. Thus, for each lizard there were five estimates of its home range, which was the area encompassing all sightings of that individual during each period. Search effort was the same on all days. A previous study of the same population showed that approximately 10 sightings for males and 6 for females described 80% of the home range estimated using all sightings, and we considered this to be the minimum number of sightings that adequately represented home-range size in this population (Martín and Salvador 1997). Thus, in this paper we use only home-range data that fulfill these requirements. Neighbors were defined as those lizards whose home ranges overlapped. When data were not normally distributed and (or) variances were not homogeneous after appropriate transformations, we used non-parametric analyses. To examine changes in home-range size and number of male or female neighbors of the same individuals through the two periods we used non-parametric Friedman's ANOVA by rank. This test assumes that the variables (levels) under consideration were measured on at least an ordinal (rank order) scale. The null hypothesis for the procedure is that the different columns of data contain samples drawn from the same population, or more specifically, populations with identical medians. Thus, the interpretation of results from this procedure is similar to that of a repeated-measures ANOVA. Pairwise comparisons a posteriori were planned using non-parametric multiple-comparison procedures (Sokal and Rohlf 1995). Reported probabilities for each set of tests were not adjusted for multiple comparisons, but the reported significance was verified where appropriate using Rice's (1989) sequential Bonferroni adjustment for multiple comparisons (Chandler 1995). In addition, we compared the home-range sizes of males and females in each period using Mann–Whitney *U* tests (Siegel and Castellan 1988). Pearson's correlations were conducted between the number of sightings or the number of individual lizards that were active each day and the sequence of the days on which fieldwork was carried out (Sokal and Rohlf 1995).

Thermal effects on activity

To examine the characteristics and seasonal changes of the thermal environment during the field study, we randomly measured the temperature (to the nearest 0.1°C) of the air, ground, and rocky soil each hour (from 08:00 to 18:00 GMT) during the first 10 days of June (mating period) and the last 10 days of July (nonmating period) using an electronic digital thermometer. Air temperature was measured 10 cm above the substrate. To avoid the influence of direct incident sunlight, an opaque lampshade was used during each measurement. We computed the mean temperature for each day and used Mann–Whitney *U* tests to compare temperatures during the mating and nonmating periods. To assess whether the thermal environment was optimal for lizard activity, we compared these temperatures with data from previous studies on the thermal biology (e.g., body temperatures of lizards measured in the field and in thermal gradients) of the same population of *L. monticola* (Carrascal et al. 1992; Martín and Salvador 1993).

Distance travelled and time spent walking

During the first week of June (mating period) and the last week of July 2000 (nonmating period) we carried out focal observations of males and females in the same study area from 09:00 to 12:00

GMT. Each lizard was followed for 5 min from a distance to avoid disturbing it; binoculars were used when necessary. Time spent walking and total distance travelled were noted for each lizard. Focal observations were terminated when lizards had been out of sight for more than 30 s or their behaviour was affected by the observer's presence. Mature males and females were easily identifiable at long range; however, lizards were captured when possible to determine sex and measure their SVL. The sex of all captured lizards coincided with that previously assigned. Given the large size of the area surveyed (more than 5 km^2) and the high lizard density, and because we avoided walking routes taken previously, the probability of repeated sampling of the same individual was very low. We therefore treated all measurements as independent. We used two-way ANOVAs to compare the time individuals spent walking and the distance travelled between males and females and between periods (Sokal and Rohlf 1995). Pairwise comparisons were made using Tukey's HSD tests.

Social interactions

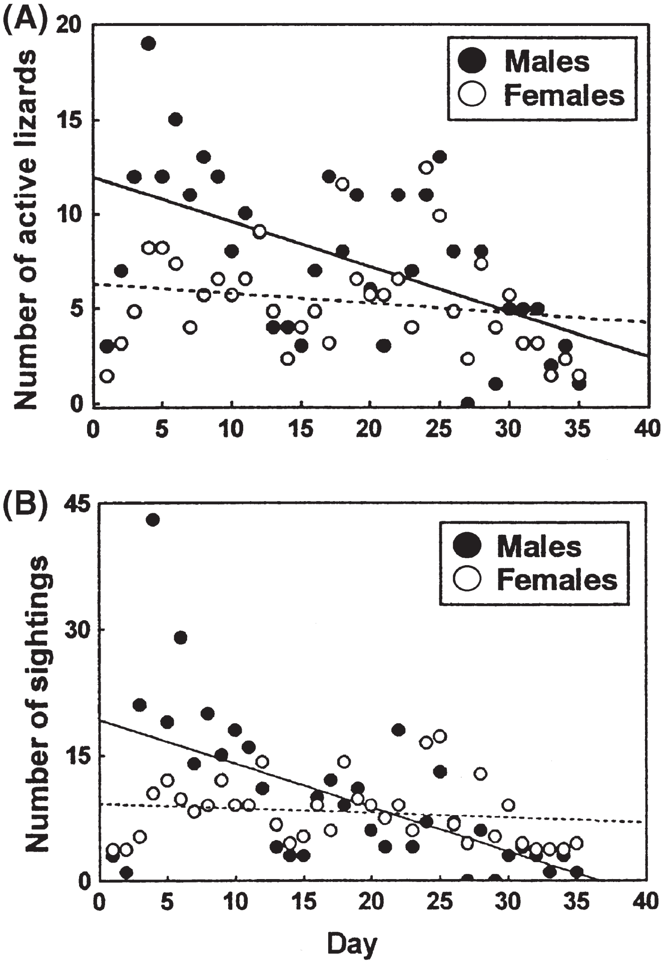
During censuses, agonistic interactions and matings were also noted. Agonistic interactions consisted mainly of chases between males, while mating interactions were those in which courtship and (or) copulation was observed. Courtship was noted when a male approached a female slowly, then gently bit her tail near the cloaca and finally copulated if she was receptive. We also noted when a male was found close to a female (less than 0.1 m away for more than 5 min) and following her movements closely, which was operationally defined as mate-guarding behavior (Olsson and Shine 1998). We used Pearson's correlations to examine the relationship between the number of agonistic interactions between males, the frequency of courtship of females, and the frequency of mate guarding observed each day and the sequence of the days on which fieldwork was carried out (Sokal and Rohlf 1995). We also compared the numbers of agonistic interactions between males, frequency of courtship of females, and frequency mate guarding observed in the year 2000 with an expected binomial distribution, assuming frequencies to be equally probable in each period (mating and nonmating).

Results

Activity and thermal environment

There was a significant negative correlation between the number of individual males that were seen active each day and the sequence of days (Pearson's correlation, $r = -0.54$, $F_{[1,33]} = 13.82$, $P < 0.001$; Fig. 1A). In contrast, there was no significant correlation in the number of active females seen active each day and the sequence of days ($r = -0.19$, $F_{[1,33]} = 1.24$, $P = 0.27$). Similarly, there was also a significant correlation between the number of total sightings of all individuals and the sequence of days for males ($r = -0.58$, $F_{[1,33]} = 17.01$, $P = 0.0002$; Fig. 1B) but not for females ($r = -0.15$, $F_{[1,33]} = 0.75$, $P = 0.39$). This decrease in the activity of males cannot be explained by thermal constraints because the temperatures of the ground (mating period: 25.6 ± 1.2°C (mean ± SE), range = 19.9–32.6°C; nonmating period: 27.7 ± 1.6°C, range = 19.2–33.9°C), rocky soil (mating period: 23.6 ± 0.7°C, range = 21.2–26.7°C; nonmating period: 25.5 ± 1.2°C, range = 17.7–29.5°C), and air (mating period: 19.2 ± 0.7°C, range = 15.0–22.4°C; nonmating period: 22.7 ± 1.2°C, range = 16.0–27.1°C) were suitable for the activity of the lizards in both periods. Thus, there were no significant differences between the mating and nonmating periods in the temperature of the ground (Mann–Whitney *U* test, $z = -1.28$, $P = 0.19$) or rocky soil ($z = -1.51$, $P = 0.13$). Air temperatures, however, were significantly higher, though more favorable for lizards' activity, in the nonmating period than in the mating period ($z = -2.19$, $P = 0.03$).

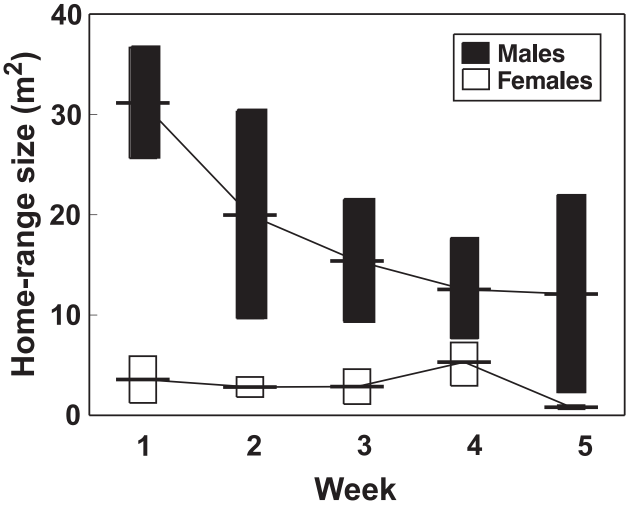
Fig. 1. Relationships between the number of active lizards (A) and the number of sightings (B) and the sequence of days for male and female *L. monticola*.



Spatial relationships

Home-range sizes varied significantly in both sexes among the five seasonal periods (Friedman's two-way ANOVA, males: $\chi^2_{[4]} = 27.43$, $P < 0.0001$; females: $\chi^2_{[4]} = 11.7$, $P = 0.02$; Fig. 2). Males' home-ranges were significantly larger in the first period than in the fourth and fifth periods (non-parametric multiple comparisons, $P < 0.001$), and also in the second period than in the fifth period ($P < 0.005$). There were no significant differences in the rest of comparisons ($P > 0.05$ in all cases). For females, the home range significantly smaller in the fifth period than in the third and fourth periods ($P < 0.005$). Similarly, there was a gradual seasonal decrease in males' home-range sizes (Pearson's correlation, $r = -0.91$, $F_{[1,33]} = 15.31$, $P = 0.02$) but not in females' ($r = -0.38$, $F_{[1,33]} = 0.49$, $P = 0.53$; Fig. 2). On the other hand, the home ranges of males were significantly larger than those of females in the first period (Mann–Whitney *U* test, $z = 4.25$, $P < 0.0001$) but not in the remaining periods ($P > 0.05$ in all cases).

Fig. 2. Seasonal changes (mean ± 1 SE) in home-range sizes of male and female *L. monticola*.



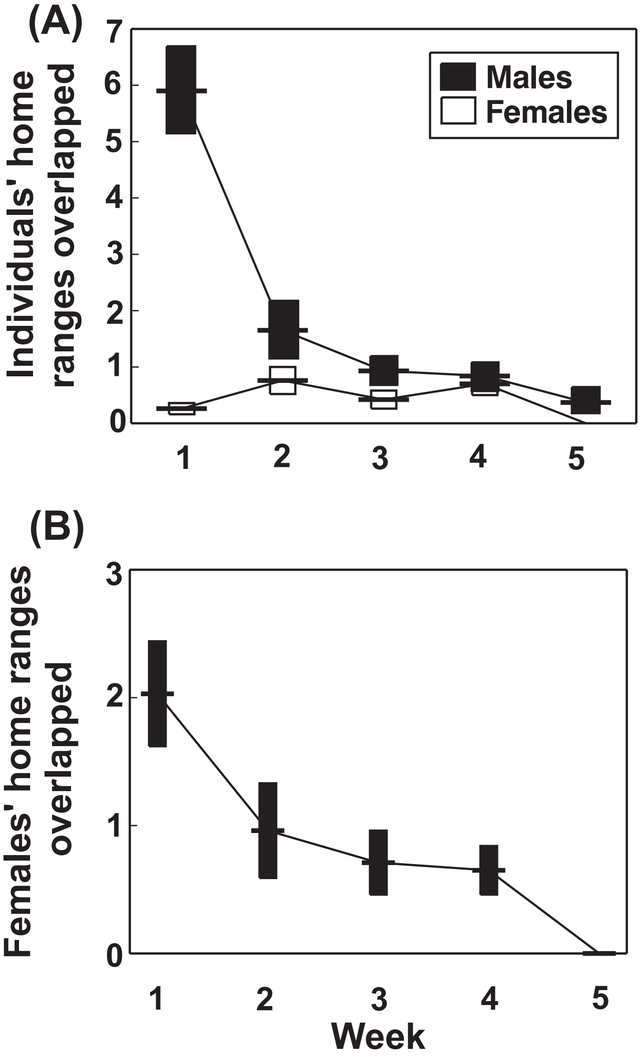
The number of same-sex neighbors varied significantly among the five periods for both sexes (Friedman's two-way ANOVA, males: $\chi^2_{[4]} = 45.41$, $P < 0.0001$; females: $\chi^2_{[4]} = 9.71$, $P < 0.05$; Fig. 3A). In the first period, the number of males' home ranges that overlapped those of other males was significantly higher than in the remaining periods (nonparametric multiple comparisons, $P < 0.001$ in all cases), and was significantly higher in the second period than in the fifth period ($P < 0.01$), but there were no significant differences between the remaining periods ($P > 0.05$). However, the number of females neighboring other females did not change significantly between periods ($P > 0.05$ in all cases). On the other hand, the number of males' home ranges overlapped by those of males varied significantly among periods (Friedman's two-way ANOVA, $\chi^2_{[4]} = 36.71$, P < 0.0001; Fig. 3B), being significantly higher in the first period than in the remaining periods ($P < 0.001$ in all cases).

The numbers of males' and females' home ranges that overlapped the home range of each male were significantly correlated in all periods except the fifth, when there were no overlapping females' home ranges (Pearson's correlations, $0.56 < r < 0.87$, $P < 0.0001$ in all cases, $N = 32$). Thus, the higher the number of female neighbors, the higher the number of male neighbors.

Distance travelled and time spent walking

Distance travelled varied significantly between periods (two-way ANOVA, $F_{[1,84]} = 23.10$, $P < 0.0001$) between the sexes ($F_{[1,84]} = 21.17$, $P < 0.0001$) and the interaction was also significant ($F_{[1,84]} = 27.19$, $P < 0.0001$; Fig. 4A). Distance travelled by males was significantly greater in the mating than in the nonmating period (Tukey's HSD test, $P < 0.001$), but there were no significant differences for females ($P = 0.99$). Distance travelled was significantly greater for males than for females in the mating period ($P < 0.001$), but there were no significant differences in the nonmating period ($P = 0.98$). Similarly, time spent walking varied significantly between periods (two-way ANOVA, $F_{[1,84]} = 23.95$, $P < 0.0001$) between the sexes ($F_{[1,84]} = 31.06$, $P < 0.0001$) and the interaction was also significant ($F_{[1,84]} = 27.35$, $P < 0.0001$; Fig. 4B). Time spent walking was significantly greater in the mating than in the nonmating period for males (Tukey's HSD test, $P < 0.001$), but there were no significant differences for females ($P = 0.99$). Time spent walking was significantly greater for males than for females in the mating period ($P < 0.001$), but there were no significant differences in the nonmating period ($P = 0.99$).

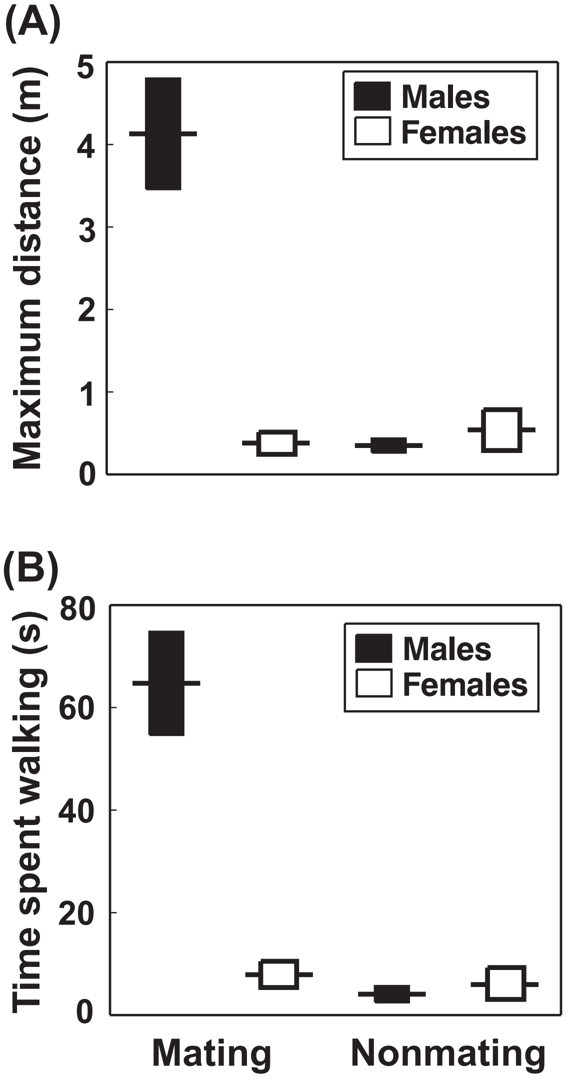
Fig. 3. Seasonal changes (mean ± 1 SE) in the number of neighbors of the same sex for male and female *L. monticola* (A) and the number of females' home ranges (mean ± 1 SE) overlapped by those of male *L. monticola* (B).



Social relationships

The number of agonistic interactions between males ($r = -0.46$, $F_{[1,33]} = 8.64$, $P = 0.005$; Fig. 5A), the frequency of courtship of females ($r = -0.49$, $F_{[1,33]} = 10.32$, $P = 0.002$; Fig. 5B) and the frequency of mate guarding ($r = -0.38$, $F_{[1,33]} = 5.46$, $P = 0.02$; Fig. 5C) decreased significantly with the sequence of days. Similarly, in the year 2000 the number of agonistic interactions (two-tailed binomial test, $P = 0.038$), frequency of courtship ($P = 0.031$), and frequency of mate guarding ($P = 0.031$) were significantly higher in the

Fig. 4. Total distance travelled (mean ± 1 SE) (A) and time spent walking (mean ± 1 SE) (B) during 5-min focal observations of male and female *L. monticola* in the mating and nonmating periods.

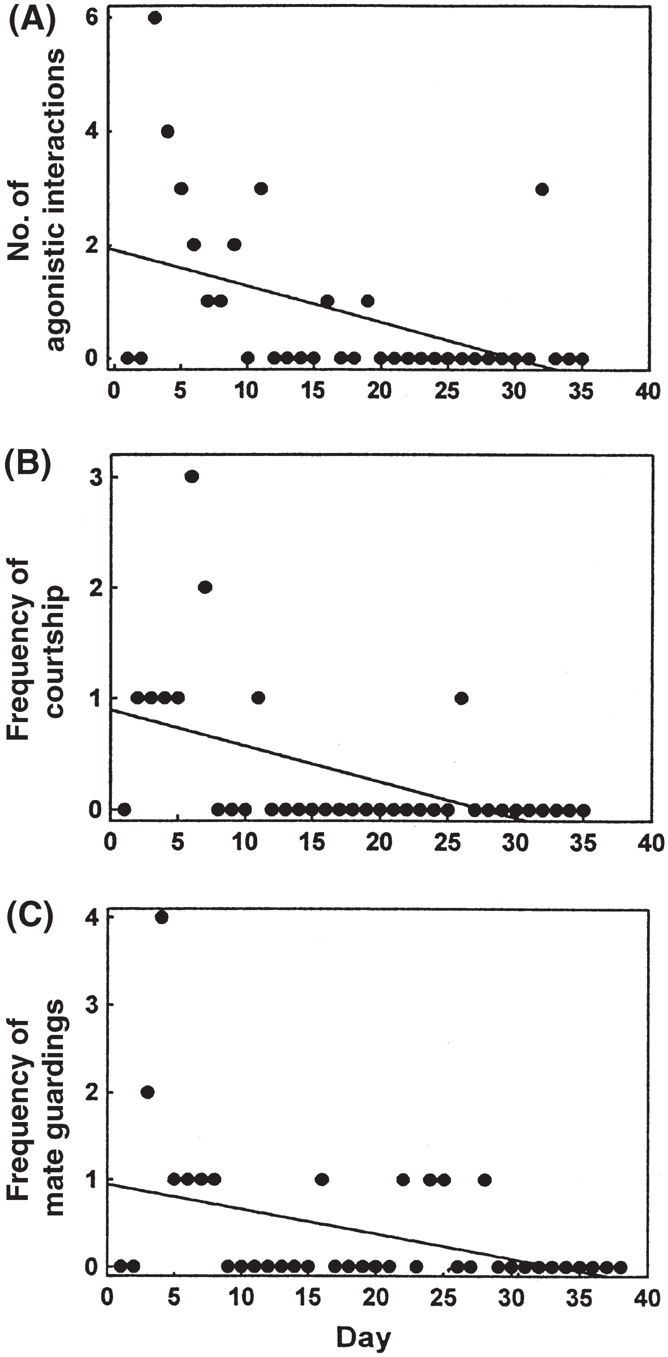


mating period (first week of June) than in the nonmating period (last week of July).

Discussion

Our results showed that the number of individual males that were seen active and the number of sightings per day decreased as the season progressed. However, we did not find such a relationship for females. This pronounced change in activity in males but not in females has also been reported in other lizards such as *Anolis nebulosus* (Lister and Aguayo 1992), *Sceloporus virgatus* (Rose 1981), *Sceloporus jarrovi* (Ruby 1978), *Sceloporus graciosus*, and *Sceloporus undulatus* (Ferguson 1971). In our study, however, these seasonal changes cannot be explained by changes in the thermal environment. The body temperatures of active *L. monticola* in this population range from 29.0 to 37.5°C (Perez-Mellado 1982; Martín and Salvador 1993), and the available ambient temperatures that we measured in our study area were equally suitable for the activity of lizards during the mating and the nonmating period. In fact, the air temperature was even more suitable for the activity of lizards in the nonmating period. In addition, if these variations in activity level depended only on temperature, seasonal changes should occur in both sexes, but females showed no significant change.

Fig. 5. Relationship between the sequence of days and the number of agonistic interactions between males (A), the frequency of courtship of females (B), and the frequency of mate guarding observed.



In male *L. monticola* there may be a trade-off between gaining access to potential mates and avoiding encounters with other males. When a male increases his home-range size in order to increase the number of neighboring females, the number of neighboring males also increases. Thus, a large home range could cause a higher probability of costly agonistic encounters. Also, the home ranges of males of the teiid lizard *Ameiva plei* overlap those of other males as frequently they overlap those of females (Censky 1995). However, when mating activity decreases, the costs of agonistic encounters should be higher because the probability of mating is lower. In fact, the numbers of both agonistic encounters and mating interactions in male *L. monticola* decrease with the sequence of days. Similarly, the frequency and intensity of intrasexual aggression are higher in the mating season than in the nonmating season for *Anolis aeneus* (Stamps and Crews 1976), *A. nebulosus* (Lister and Aguayo 1992), and *S. jarrovi* (Ruby 1978). Interestingly, a study performed with a population of *S. undulatus*, whose breeding season ends in June, as in *L. monticola*, showed that males performed fewer push-up and head-shake displays in early July, and performed less consistently than in late June (Klukowski and Nelson 1998). Even if these changes are due to a decrease in aggressiveness per se, it is unlikely that this would occur in all individuals simultaneously. Thus, if a male with a low level of aggressiveness encountered another male with a higher level of aggressiveness, this would pose a risk of injury to the former. Therefore, our results suggest the existence of other mechanisms for reducing aggressive encounters. Males, but not females, decreased their home-range size throughout the periods, and the home ranges of males were larger than those of females only at the beginning of the mating season, when most social interactions between the sexes occurred. Also the home ranges of male *S. jarrovi* (Ruby 1978), *S. undulatus* (Ferner 1974), *A. nebulosus* (Lister and Aguayo 1992), *A. aeneus* (Stamps and Crews 1976), and *Anolis cupreus* (Fleming and Hooker 1975) were larger in the mating period than in the nonmating period. During the mating period, the greater distance travelled and longer time spent walking by males, but not by females, suggest that male *L. monticola* travel farther from their home-range centers in order to increase their access to potential mates. In fact, the number of females' home ranges that were overlapped by a male's home range at the beginning of the mating season is higher than in other periods. Similarly, male *S. undulatus* moved less often and moved a shorter total distance in early July than in late June (Klukowski and Nelson 1998).

The number of home ranges of male *L. monticola* that overlapped the home range of each male is higher during the part of the activity season when most mating interactions occur. In contrast, other studies reported that this pattern of overlapping ranges shifted to non-overlapping in the mating season in *A. cupreus* (Fleming and Hooker 1975) and *S. jarrovi* (Ruby 1978) because home ranges were defended against intrusions by other males. However, the greater overlap between males' home ranges in the mating season might be a system that favors dominant or high-status male *L. monticola*, which would be able to increase their mating success by enlarging their home ranges in order to overlap the home ranges of low-status or subordinate individuals. On the other hand, since males increase their home range in order to overlap the home ranges of more females, and because they probably cannot prevent other males from mating with females when they are not present, an adaptive strategy might be to guard the females while they are receptive. Similar mate-guarding strategies are useful for avoiding extra-pair matings and insuring paternity (Sherman 1989; Birkhead and Møller 1992), and have been reported in other teids (Censky 1995) and lacertids (Olsson 1993). In fact, we observed that when mating activity decreased, the number of observations in which a male was close to a female also decreased.

We conclude from the results of this study, taken together, that the balance between the benefits and costs of activity may differ seasonally in males but are apparently similar in females. Thus, the fact that the number of aggressive interactions between males declined in the nonmating season suggests that the adaptive significance of these interactions is to increase males' mating success. However, when the mating season ends, males would be expected to derive no benefits from additional matings, and may be able to reduce the costs of aggressive encounters by reducing their activity and spatial overlap with other males at this time. An alternative, but not mutually exclusive, explanation is that males may minimize the risk of predation by reducing activity levels, as has been suggested for *A. nebulosus* (Lister and Aguayo 1992), *Corytophanes cristatus* (Andrews 1979), and *S. virgatus* (Rose 1981).

Acknowledgments

We thank two anonymous reviewers for their helpful comments, and El Ventorrillo Field Station (MNCN) for the use of their facilities. Financial support was provided by Dirección General de Enseñanza Superior e Investigación Científica project PB-98-0505 and a CSIC contract to P.L.

References

Andrews, R.M. 1979. The lizard *Corytophanes cristatus*: an extreme 'sit and wait' predator. Biotropica, **11**: 136–139.

Birkhead, T.R., and Møller, A.P. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London.

Carrascal, L.M., López, P., Martín, J., and Salvador, A. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. Ethology, **92**: 143–154.

Censky, E.J. 1995. Mating strategy and reproductive success in the teiid lizard, *Ameiva plei*. Behaviour, **132**: 529–557.

Chandler, C.R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. Anim. Behav. **49**: 524–527.

Elvira, B., and Vigal, C.R. 1985. Further data on the reproduction of *Lacerta monticola cyreni* (Sauria, Lacertidae) in central Spain. Amphib.-Reptilia, **6**: 173–179.

Ferguson, G.W. 1971. Observations of the behavior and interactions of two sympatric *Sceloporus* in Utah. Am. Midl. Nat. **86**: 190–196.

Ferner, J.W. 1974. Home range size and overlap in *Sceloporus erythroceilus*. Copeia, 1974: 332–337.

Fleming, T.H., and Hooker, R.S. 1975. *Anolis cupreus*: the response of a lizard to tropical seasonality. Ecology, **56**: 1243–1261.

Foà, A., Monteforti, G., Minutini, L., Innocenti, A., Quaglieri C., and Flamini, M. 1994. Seasonal changes of locomotor activity patterns in ruin lizards *Podarcis sicula* I. Endogenous control by the circadian system. Behav. Ecol. Sociobiol. **34**: 267–274.

Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. *In* Biology of the Reptilia. Vol. 12. *Edited by* C. Gans and F.H. Pough. Academic Press, London and New York. pp. 25–91.

Innocenti, A., Minutini, L., and Foà, A. 1994. Seasonal changes of locomotor activity patterns in ruin lizards *Podarcis sicula* II. Involvement of the pineal. Behav. Ecol. Sociobiol. **35**: 27–32.

Klukowski, M., and Nelson, C.E. 1998. The challenge hypothesis and seasonal changes in aggression and steroids in male northern fence lizards (*Sceloporus undulatus hyacinthinus*). Horm. Behav. **33**: 197–204.

Labra, A., and Rosenmann, M. 1992. Comparative diel activity of *Pristidactylus* lizards from forest and scrubland habitats. J. Herpetol. **26**: 501–503.

Larkin, R.P., and Halkin, D. 1994. A review of software packages for estimating animal home ranges. Wildl. Soc. Bull. **22**: 274–287.

Lister, B.C., and Aguayo, A.G. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. J. Anim. Ecol. **61**: 717–733.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends Ecol. Evol. **6**: 183–186.

Marler, C.A., and Moore, M.C. 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. Behav. Ecol. Sociobiol. **23**: 21–26.

Martín, J., and López, P. 2000. Social status of male Iberian rock lizards (*Lacerta monticola*) influence their activity patterns during the mating season. Can. J. Zool. **78**: 1105–1109.

Martín, J., and Salvador, A. 1992. Tail loss consequences on habitat use by the Iberian rock-lizard, *Lacerta monticola*. Oikos, **65**: 318–324.

Martín, J., and Salvador, A. 1993. Thermoregulatory behaviour of rock lizards in response to tail loss. Behaviour, **124**: 123–136.

Martín, J., and Salvador, A. 1997. Effects of tail loss on the time budgets, movements, and spacing patterns of Iberian rock lizards, *Lacerta monticola*. Herpetologica, **53**: 117–125.

Olsson, M. 1993. Contest success and mate guarding in male sand lizards, *Lacerta agilis*. Anim. Behav. **46**: 408–409.

Olsson, M., and Shine, R. 1998. Chemosensory may recognition may facilitate prolonged mate guarding by snow skinks, *Niveoscincus microlepidotus*. Behav. Ecol. Sociobiol. **43**: 359–363.

Perez-Mellado, V. 1982. Datos sobre *Lacerta monticola* Boulenger 1905 (Sauria, Lacertidae) en el oeste del Sistema Central. Doñana Acta Vertebr. **9**: 107–130.

Porter, W.P., and Tracy, C.R. 1983. Biophysical analyses of energetics, time–space utilization and distributional limits. *In* Lizard ecology: studies of a model organism. *Edited by* R.B. Huey, E.R. Pianka, and T.W. Schoener. Harvard University Press, Cambridge, Mass. pp. 55–83.

Porter, W.P., Mitchell, J.W., Beckman, W.A., and de Witt, C.B. 1973. Behavioral implications of mechanistic ecology: thermal and behavioral modeling of desert ectotherms and their microenvironment. Oecologia, **12**: 1–54.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**: 223–225.

Rose, B. 1981. Factors affecting activity in *Sceloporus virgatus*. Ecology, **62**: 706–716.

Rose, B. 1982. Lizard home ranges: methodology and function. J. Herpetol. **16**: 253–269.

Ruby, D.E. 1978. Seasonal changes in the territorial behavior of the iguanid lizard *Sceloporus jarrovi*. Copeia, 1978: 430–438.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology, **51**: 408–418.

Sherman, P. 1989. Mate guarding as paternity insurance in Idaho ground squirrels. Nature (Lond.), **388**: 418–420.

Siegel, S., and Castellan, N.J. 1988. Nonparametric statistics for the behavioral sciences. 2nd ed. McGraw–Hill, New York.

Simon, C.A., and Middendorf, G.A. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. Ecology, **57**: 1317–1320.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd. ed. W.H. Freeman and Co., New York.

Sound, P., and Veith, M. 2000. Weather effects on microhabitat movements of the western green lizard, *Lacerta binileata* (Daudin, 1802), at its northern distribution range border: a radio-tracking study. Can. J. Zool. **78**: 1831–1839.

Stamps, J.A. 1983. Sexual selection, sexual dimorphism and territoriality. *In* Lizard ecology: studies of a model organism. *Edited by* R.B. Huey, E.R. Pianka, and T.W. Schoener. Harvard University Press, Cambridge, Mass. pp. 169–204.

Stamps, J.A., and Crews, D.P. 1976. Seasonal changes in reproduction and social behavior in the lizard *Anolis aeneus*. Copeia, 1976: 467–476.