

# Lipophilic Compounds from the Femoral Gland Secretions of Male Hungarian Green Lizards, *Lacerta viridis*

Renata Kopena<sup>a</sup>, Pilar López<sup>b</sup>, and José Martín<sup>b,\*</sup>

<sup>a</sup> Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Faculty of Science, Eötvös Loránd University, Pázmány Péter s 1/C, H-1117 Budapest, Hungary

<sup>b</sup> Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain. Fax: 34-91-5 64 50 78. E-mail: Jose.Martin@mncn.csic.es

\* Author for correspondence and reprint requests

Z. Naturforsch. **64c**, 434–440 (2009); received February 27, 2009

In spite of the importance of chemical signals (pheromones) in the reproductive behaviour of lizards, only a few studies have examined the role of specific chemical compounds as sexual signals. The secreted chemicals vary widely between species but whether this variation reflects phylogenetic or environmental differences remains unclear. Based on mass spectra, obtained by GC-MS, we found 40 lipophilic compounds in femoral gland secretions of male green lizards (*Lacerta viridis*), including several steroids,  $\alpha$ -tocopherol, and esters of  $n$ -C<sub>16</sub> to  $n$ -C<sub>20</sub> carboxylic acids, and minor components such as alcohols between C<sub>12</sub> and C<sub>20</sub>, squalene, three lactones and one ketone. We compared these chemicals with those previously found in other closely related green lizard species, and discussed how phylogenetical differences and/or environmental conditions could be responsible for the differential presence of chemicals in different lizard species.

**Key words:** *Lacerta viridis*, Waxy Esters, Steroids, Tocopherol

## Introduction

Intraspecific communication by chemical signals (pheromones) plays a main role in social organization and sexual selection of many reptiles (Mason, 1992). Males of many lizard species secrete chemicals from the femoral glands that may function as pheromones (Alberts, 1993; Weldon *et al.*, 2008). The presence and relative concentration of pheromone components in femoral secretions seem to vary consistently among individuals and might transmit chemical information about the characteristics and health state of a male (López *et al.*, 2006; Martín *et al.*, 2007a). Behavioural experiments found evidence of female preferences for substrates scent marked by particular individual males, which suggest active pheromonal mate choice (*e.g.*, Martín and López 2000, 2006a; López *et al.*, 2002, 2003; Olsson *et al.*, 2003; López and Martín, 2005a). Substrate scent marks can also provide information to other males on individuality, fighting ability or dominance status (Aragón *et al.*, 2001; Carazo *et al.*, 2007; Martín *et al.*, 2007b).

However, there is little knowledge on the role of specific chemical compounds as sexual signals in lizards. The chemical composition of femoral gland secretions has been analyzed in only a few lizard species (reviewed in Weldon *et al.*, 2008). Secretions are composed of both lipids and proteins, but most recent evidences point to lipids as the main compounds involved in pheromonal communication (Mason, 1992; Martín and López, 2006a). The few informations available on the chemical composition of femoral secretions indicate that although the types of chemicals in secretions are similar (*e.g.* steroids, carboxylic acids and alcohols, among others), the presence of specific compounds and the relative proportion of each chemical vary widely between species. These variations may be due to phylogenetic differences between species *per se*, but it is also likely that, if the persistence of scent marks in the habitat is a requisite for their efficiency, there is selection for the presence of different chemicals with different properties in different habitats (Alberts, 1992; Escobar *et al.*, 2003; Martín and López, 2006b). However, to test this hypothesis, we need more studies that deal with a wider range of lizard taxa

and consider a larger variety of microhabitat and environmental conditions.

“Green lizards” are a distinctive clade of lacertid lizard species (Harris *et al.*, 1998; Godinho *et al.*, 2005) with adult males often having green brilliant dorsal colourations (Václav *et al.*, 2007). They are large and robust lizards that tend to live in dense vegetation. Several closely related species of green lizards are widely distributed throughout much of the southern half of Europe, from France and Spain, through Central Europe to the Black sea, the Balkans and Greece, thus inhabiting a wide range of environmental conditions (Nettman and Rykena, 1984; Arnold and Ovenden, 2002; Böhme *et al.*, 2007). There are no specific studies on chemosensory detection of conspecific scents in green lizards, but, as in other lacertid lizards, the vomeronasal organ is well developed and chemoreceptor cells are abundant (Cooper, 1996), tongue-flicking is often observed during social interactions (unpublished observations), and there is a clear sexual dimorphism in femoral pores, *i.e.*, the size of pores, and the amount of secretion is higher in adult males and during the mating season; females have vestigial pores without apparent secretion. These data strongly suggests that, as in other lacertids, green lizards should use femoral gland chemical secretions in some aspects of their reproduction and social life.

A previous study examined the femoral gland secretions of the Schreiber’s green lizard (*Lacerta schreiberi*) (López and Martín, 2006), an endemic lizard from the North and Central Iberian Peninsula. Secretions of this lizard include several steroids,  $\alpha$ -tocopherol, and  $n$ -C<sub>9</sub> to  $n$ -C<sub>22</sub> carboxylic acids and their esters, and minor components such as alcohols between C<sub>12</sub> and C<sub>24</sub>, two lactones, two ketones, and squalene (López and Martín, 2006).

In the present paper, we report the results of an analysis by gas chromatography-mass spectrometry (GC-MS) of the lipophilic fraction of femoral secretions of male green lizards (*Lacerta viridis*) from a Hungarian population. This is a large diurnal lacertid lizard, widespread in Europe, from Turkey and the Balkan Peninsula northwards across the Carpathian Basin to Ukraine, the Czech Republic and eastern Germany (Nettman and Rykena, 1984; Böhme *et al.*, 2007). In Hungary, the subspecies *L. v. viridis* is found in almost all its territory from plains to mountains, in open woods, woods and field edges (Puky *et al.*, 2005).

In spring males defend territories from other males, the centre of the territory being the main refuge (Ihász *et al.*, 2006). We compared the current data on femoral secretions of *L. viridis* with previous data on the related *L. schreiberi* (López and Martín, 2006), aiming to understand whether the patterns of the lipid composition of femoral secretions of different lizard species depend on taxonomic affinities and/or environmental characteristics.

## Material and Methods

We captured by noosing 22 adult male *L. viridis* during April and May 2007 and 2008, from a population near Tápiószentmárton (Pest county, Hungary). The habitat is sand puszta with disturbed grassland, cultivated sand cottonwoods, honey locust (*Gleditsia triacanthos*) scrub, and artificially planted black pine forests (*Pinus nigra*). The soil is sandy with a large grass cover, where invasive weeds dominate. Only adult lizards with intact or fully regenerated tails were considered. Lizards were weighed [body mass, (16.5 ± 5.6) g; range, 6.3–27.7 g] and their snout-vent length (SVL) was measured [mean ± SE, (83 ± 9) mm; range, 64–100 mm]. Lizards had an average (± SE) of (17 ± 1) (range, 15–20) femoral pores on each leg.

We extracted the femoral pores secretion of lizards by gently pressing around the femoral pores with a forceps, and collected the secretion directly in glass vials with Teflon-lined stoppers. The vials were stored at –20 °C until analyses. Lizards were released to their initial sighting location prior to the capture. We also used the same procedure on each sampling occasion, but without collecting secretion, to obtain blank control vials that were treated in the same manner to compare with the lizards samples and be able to exclude contaminants from the handling procedure or from the environment, where lizards were found, and for further examining impurities in the solvent.

We analyzed the samples with a Finnigan-ThermoQuest Trace 2000 gas chromatograph (GC) fitted with a poly(5% diphenyl/95% dimethylsiloxane) column (Supelco, Equity-5, 30 m length × 0.25 mm ID, 0.25 μm film thickness) and a Finnigan-ThermoQuest Trace 2000 mass spectrometer (MS) as detector. The samples, 2 ml of each sample dissolved in *n*-hexane (Sigma, capillary GC grade), were injected using the splitless

mode at an inlet temperature of 250 °C. The GC was programmed so that the oven temperature was kept at 50 °C for 10 min, increased to a final temperature of 280 °C at a rate of 5 °C/min, and kept at this temperature for 30 min. The carrier gas was helium at 30 cm/s. Ionization by electron impact (70 eV) was carried out at 280 °C. Mass spectral fragments below  $m/z = 39$  were not recorded. Impurities identified in the solvent and/or the control vial samples are not reported. Initial identification of secretion components was performed by comparison of sample mass spectra with those in the NIST/EPA/NIH 1998 computerized mass spectral library. If possible, identifications were confirmed by comparison of spectra and retention times with those of authentic standards (from Sigma-Aldrich Chemical Co).

## Results and Discussion

A total of 40 lipophilic compounds were identified in femoral gland secretions of male *L. viridis* (Table I). The main components were steroids (59.6% of TIC),  $\alpha$ -tocopherol and one of its derivatives (28.5%), esters of carboxylic acids ranging between  $n$ -C<sub>16</sub> and  $n$ -C<sub>20</sub> (4.6%), five alcohols between C<sub>12</sub> and C<sub>20</sub> and two unidentified alcohol derivatives (2.6%), and squalene (2.5%), but we also found three lactones (1.6%), one ketone (0.2%), and one unidentified, but characteristic compound (0.4%). The major compounds were detected in all individuals, although the relative proportions of some chemicals showed a high interindividual variability. On average, the two most abundant chemicals were cholestan-3-one (27.5% of TIC) and  $\alpha$ -tocopherol (25.6%), followed by lower amounts of cholesteryl methyl ether (6.7%), cholest-4-en-3-one (5.9%) and cholesta-3,5-dien-7-one (5.8%).

We found a high portion of  $\alpha$ -tocopherol in secretions of this lizard. Similarly, in secretions of the closely related Schreiber's green lizard (*L. schreiberi*),  $\alpha$ -tocopherol was also the main compound (18.3%) (López and Martín, 2006). Both, the similar microhabitats and the close phylogenetic relationship between these two green lizards may explain the presence of large amounts of  $\alpha$ -tocopherol in the secretions.  $\alpha$ -Tocopherol was also found, although in much less amounts (between 0.1 and 1.9%), in femoral secretions of the European lacertid, but unrelated, lizards *Acanthodactylus erythrurus*, *Psammodromus algerus*,

*Podarcis muralis* and *Lacerta vivipara* (López and Martín, 2005b; Martín and López, 2006b, c; Gabirrot *et al.*, 2008), and also in the South African cordylid, *Cordylus giganteus* (Louw *et al.*, 2007). Furthermore, other unrelated reptiles such as amphisbaenians and crocodiles also have  $\alpha$ -tocopherol in their glandular secretions (López and Martín, 2005c; Weldon *et al.*, 1987, 1988). This suggests that the presence of  $\alpha$ -tocopherol in secretions is not just a consequence of the close phylogenetic relationship between green lizard species.

$\alpha$ -Tocopherol, and also squalene, are two well known fixers and lipophilic antioxidants (Brigelius-Flohe and Traber, 1999), whose first possible function in secretions might be to inhibit oxidation of other glandular lipid components in the wet environments usually occupied by both species of green lizards, *L. viridis* and *L. schreiberi*, and to increase the chemical stability of the other lipid fractions in scent marks by limiting oxidation (see Alberts, 1992; Novotny and Martín-Neto, 2002).

However, secretion of  $\alpha$ -tocopherol has to be costly for lizards. First,  $\alpha$ -tocopherol is typically produced by microorganisms and plants, and thus should be dietary in origin. Furthermore,  $\alpha$ -tocopherol is one of the most abundant forms of vitamin E, which is the main lipophilic antioxidant and radical scavenger, both *in vitro* and *in vivo*, and it is involved in membrane defense (Burton and Traber, 1990; Brigelius-Flohe and Traber, 1999). The physiological relevance and the severe pathological consequences of  $\alpha$ -tocopherol deficiency, such as neurological disorders or lung diseases, impose a major challenge to animals for sustaining an adequate supply of this vitamin to different tissues (Mardones and Rigotti, 2004), particularly those highly sensitive to  $\alpha$ -tocopherol deficiency such as the brain and gonads. Given all these important functions of  $\alpha$ -tocopherol in metabolism, and given that it can only be obtained from the diet, its actual function in femoral secretions is of enough importance to divert it from metabolism and "secrete" it from the body. It is likely that only males with an adequate supply could do it, and, as it occurs in other lizards, the presence of "costly" compounds (*e.g.*, vitamin E, pro-vitamin D) in scent marks of males may be used by females as an index of the quality of a male or of his territory, which can affect female mate choice decisions (Martín and López, 2006a,d). Nevertheless, the function of  $\alpha$ -toco-

Table I. Lipophilic compounds found in femoral secretions of male green lizards, *Lacerta viridis*. The relative amount of each component was determined as the percentage of the total ion current (TIC) and reported as the average ( $\pm 1$  SE) for 22 individuals. Characteristic ions ( $m/z$ ) are reported for some unidentified compounds.

RT <sup>a</sup> [min]	Compound	Mean $\pm$ SE
30.5	Dodecanol	0.75 $\pm$ 0.37
35.1	Tetradecanol	0.17 $\pm$ 0.10
35.3	2-Pentadecanone	0.22 $\pm$ 0.16
40.0	Hexadecanol	0.33 $\pm$ 0.31
41.3	Unidentified alcohol derivative 1	0.19 $\pm$ 0.17
41.9	Hexadecanoic acid 1-methylethyl ester	0.35 $\pm$ 0.30
42.0	Heptadecanol	0.44 $\pm$ 0.20
43.0	Unidentified alcohol derivative 2	0.19 $\pm$ 0.08
43.3	Octadecenoic acid methyl ester	0.11 $\pm$ 0.06
43.4	4-Hydroxy-hexadecanoic acid $\gamma$ -lactone	0.87 $\pm$ 0.33
43.6	Octadecanol	0.36 $\pm$ 0.15
45.6	Unidentified waxy ester 1	0.09 $\pm$ 0.06
47.0	4-Hydroxy-octadecanoic acid $\gamma$ -lactone	0.59 $\pm$ 0.97
47.3	Eicosanol	0.16 $\pm$ 0.13
47.7	5-Hydroxy-octadecanoic acid $\delta$ -lactone	0.19 $\pm$ 0.18
48.3	Eicosanoic acid	0.57 $\pm$ 0.28
49.9	Hexadecanoic acid tetradecyl ester	1.05 $\pm$ 1.27
54.8	Squalene	2.46 $\pm$ 1.80
57.6	Unidentified waxy ester 2	0.54 $\pm$ 0.98
57.9	6- <i>O</i> -Methyl- $\alpha$ -tocopherol	2.82 $\pm$ 1.42
58.1	Unidentified compound (205, 430)	0.38 $\pm$ 0.28
58.3	Cholesteryl methyl ether	6.74 $\pm$ 2.64
59.7	$\alpha$ -Tocopherol	25.63 $\pm$ 10.42
60.2	Cholesta-3,5-dien-7-one	5.78 $\pm$ 2.64
60.4	Cholestan-3-one	27.45 $\pm$ 5.45
60.6	Unidentified steroid (161, 187, 355, 394, 430)	3.16 $\pm$ 1.22
61.0	Unidentified waxy ester 3	0.76 $\pm$ 0.69
61.4	Ergost-22-en-3-ol	1.27 $\pm$ 1.20
61.5	Unidentified steroid (187, 213, 255, 382, 397)	1.02 $\pm$ 0.78
61.7	Unidentified waxy ester 4	0.46 $\pm$ 0.53
62.1	Cholest-4-en-3-one	5.92 $\pm$ 3.97
62.5	Ergostanol	0.73 $\pm$ 0.47
62.8	Cholestan-3-one methyl derivative? (217, 231, 386, 401)	2.78 $\pm$ 0.81
65.0	Cholest-4-en-3-one methyl derivative? (124, 229, 275, 356, 399)	1.30 $\pm$ 0.88
65.2	Cholestan-3-one derivative? (217, 231, 386, 400, 415)	1.94 $\pm$ 0.55
65.9	Unidentified steroid (354, 380, 400, 413)	0.17 $\pm$ 0.15
66.3	Unidentified steroid (137, 245, 354, 380, 401, 413)	0.77 $\pm$ 0.37
66.8	Unidentified waxy ester 5	0.29 $\pm$ 0.26
67.8	Stigmast-4-en-3-one	0.59 $\pm$ 0.33
69.3	Unidentified waxy ester 6	0.42 $\pm$ 0.31

<sup>a</sup> RT, retention time.

pherol and other compounds in secretions remains to be analyzed properly.

In addition to  $\alpha$ -tocopherol, we found a derivative of this compound. Based on its characteristic mass spectrum (Fig. 1) we tentatively identified it as a tocopherol derivative since the difference in the ion series is similar ( $444 - 179 = 265$ ) to the difference for  $\alpha$ -tocopherol (430 and 165) and

$\gamma$ -tocopherol (416 and 151). The mass shift of the small ion of 14 amu, which represents the chromanol head portion of the tocopherol structure, suggests a methyl derivative of this group. Since there is only one likely place for methylation (the phenolic OH), the spectrum coincides with the chemical structure of 6-*O*-methyl- $\alpha$ -tocopherol. This  $\alpha$ -tocopherol derivative seems to be the

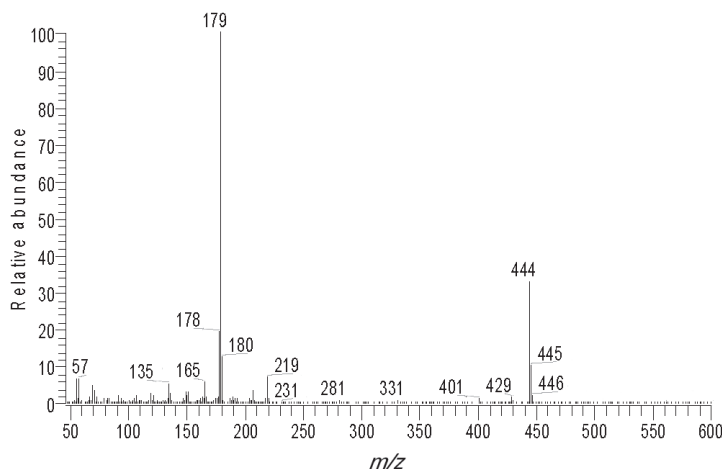


Fig. 1. Mass spectrum of the  $\alpha$ -tocopherol derivative, tentatively identified as 6-*O*-methyl- $\alpha$ -tocopherol, found in femoral secretions of male green lizards, *Lacerta viridis*.

same compound that remained unidentified in *L. schreiberi* previous analyzed (López and Martín, 2006). To our knowledge this compound has not been described as a natural product, although it can be synthesized in the laboratory, for example by treating  $\alpha$ -tocopherol with diazomethane (Saladino *et al.*, 2008). However, the simple analytical procedures that we used and the recurrent appearance of this compound in all samples of several lizard species, and in different years, made very unlikely that this compound was an artifact of our analyses.

The major steroids found in femoral secretions of *L. viridis* were different from those found in the related *L. schreiberi*. The main steroids in *L. viridis* were cholestan-3-one and cholesteryl methyl ether, whereas these two steroids are minor components in secretions of *L. schreiberi* consisting mainly of ergosterol (16%), cholestanol (12%) and a derivative of cholestanol (13%) (López and Martín, 2006). Moreover, in *L. viridis* cholestanol was not found and ergosterol was only a minor component. Also, many others of the minor steroids are different in both species. In contrast, in other lacertid lizards, cholesterol was the main steroid, and the main lipid, and it was found in high abundance: 67% in *Lacerta monticola* (López and Martín, 2005 d), between 52 and 63% in several species of *Podarcis* lizards (Martín and López, 2006b), and 86% in *Lacerta vivipara* (Gabirot *et al.*, 2008). Cholesterol was also found in *L. schreiberi*, but in considerably lower por-

tion (6.4%) (López and Martín, 2006), and was not found in *L. viridis*. These large disparities in major steroids of femoral secretions suggest that phylogenetic relationships might not explain *per se* the specific compounds found in secretions.

Interestingly, further evidence of the role of the environment regarding the composition of secretions may originate from interspecific differences in the fatty acid composition of green lizards. While, *L. viridis* secretions contain esters of C<sub>16</sub> to C<sub>20</sub> carboxylic acids and at least six waxy esters, *L. schreiberi* secretions contain free carboxylic acids between C<sub>9</sub> to C<sub>22</sub> and none waxy ester (López and Martín, 2006). Fatty acids with a higher number of carbon atoms and waxy esters are less volatile and would confer more stability to secretions under conditions where high levels of humidity increase evaporation (Alberts, 1992). Although both lizard species occupy relatively humid microhabitats, differences in the prevailing climate in the geographical areas occupied by each species might influence the chemical composition of secretions. This might be explained by the persistence of scent marks in the habitat which is important for the efficiency of intraspecific communication (Alberts, 1992). Similarly, populations of the Iberian wall lizard, *Podarcis hispanica*, that occupy areas characterized by high levels of humidity have femoral secretions with less volatile compounds (*i.e.* more waxy esters and fatty acids of longer chain) than populations of the same



species occupying drier areas (Martín and López, 2006b).

In contrast, the two green lizard species have very similar alcohols in femoral secretions, although *L. viridis* has two probable alcohol derivatives not found in *L. schreiberi*. Similar alcohols have been found in other lacertid lizards, but not in iguanian lizards (see Weldon *et al.*, 2008 for a review). Thus, it seems that alcohols might be characteristic of femoral secretions of lacertids lizards (Scleroglossa clade), but be absent in others groups (Iguania clade). Finally, both green lizard species coincide in the presence of two lactones and one ketone (López and Martín, 2006), but *L. viridis* has an additional exclusive lactone and *L. schreiberi* an additional exclusive ketone.

Further studies are clearly needed to understand the patterns of presence and abundance of different compounds in femoral secretions of lizards, and how phylogenetic relationships and environmental conditions can explain the characteristics of these secretions. Given the wide distribution of *L. viridis* in Europe, where several authors have described five subspecies, as well as other very closely related species (Nettman and Rykena, 1984; Böhme *et al.*, 2007), green lizards could be an ideal species group to examine the

causes of possible variations in femoral secretions though all their geographical range of occurrence. Also, we need to clarify the possible role of the compounds found in femoral secretions with potential of being signaling pheromones, such as tocopherol, in social organization and sexual selection processes of green lizards.

#### Acknowledgements

We thank Janos Török for useful advice and support, Katalin Bajer and Orsolya Molnár for helping in the field, and Elena Ibáñez (Instituto de Fermentaciones Industriales, CSIC), Maret G. Traber and Fred Stevens (Oregon State University), and Jeffrey Atkinson (Brock University, Ontario) for helping us to identify the tocopherol derivative. Financial support was provided by the projects MEC-CGL2005-00391/BOS and MCI-CGL2008-02119/BOS, and by a Hungarian-Spanish Intergovernmental S&T Cooperation Programme (HH2006-0024) funded by the Spanish Ministerio de Educación y Ciencia and the Hungarian Science and Technology Foundation. Captures were performed under licence of the National Inspectorate for Environment, Nature and Water of Hungary.

- Alberts A. C. (1992), Constraints on the design of chemical communication systems in terrestrial vertebrates. *Am. Nat.* **139**, 62–89.
- Alberts A. C. (1993), Chemical and behavioral studies of femoral gland secretions in iguanid lizards. *Brain Behav. Evol.* **41**, 255–260.
- Aragón P., López P., and Martín J. (2001), Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards: implications of field spatial relationships between males. *Behav. Ecol. Sociobiol.* **50**, 128–133.
- Arnold E. N. and Oviden D. W. (2002), *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. Harper Collins, London.
- Böhme M. U., Fritz U., Kottenko T., Džukic G., Ljubisavljevic K., Tzankov N., and Berendonk T. U. (2007), Phylogeography and cryptic variation within the *Lacerta viridis* complex (Lacertidae, Reptilia). *Zool. Scr.* **36**, 119–131.
- Brigelius-Flohe R. and Traber M. G. (1999), Vitamin E: function and metabolism. *FASEB J.* **13**, 1145–1155.
- Burton G. W. and Traber M. G. (1990), Vitamin E: antioxidant activity, biokinetics, and bioavailability. *Annu. Rev. Nutr.* **10**, 357–382.
- Carazo P., Font E., and Desfilis E. (2007), Chemosensory assessment of rival competitive ability and scent mark function in a lizard (*Podarcis hispanica*). *Anim. Behav.* **74**, 895–902.
- Cooper Jr. W. E. (1996), Preliminary reconstructions of nasal chemosensory evolution in Squamata. *Amph.-Rept.* **17**, 395–415.
- Escobar C. M., Escobar C. A., Labra A., and Niemeyer H. M. (2003), Chemical composition of precloacal secretions of two *Liolaemus fabiani* populations: are they different? *J. Chem. Ecol.* **29**, 629–638.
- Gabirot M., López P., Martín J., de Fraipont M., Heulin B., Sinervo B., and Clobert J. (2008), Chemical composition of femoral secretions of oviparous and viviparous types of male common lizards *Lacerta vivipara*. *Biochem. Syst. Ecol.* **36**, 539–544.
- Godinho R., Crespo E. G., Ferrand N., and Harris D. J. (2005), Phylogeny and evolution of the green lizards, *Lacerta* spp. (Squamata: Lacertidae) based on mitochondrial and nuclear DNA sequences. *Amph.-Rept.* **26**, 271–430.
- Harris D. J., Arnold E. N., and Thomas R. H. (1998), Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proc. R. Soc. London B* **265**, 1939–1948.
- Ihász N., Bajer K., Kopena R., Molnár O., Herczeg G., and Török J. (2006), Szemben a ragadozóval – a zöld gyík (*Lacerta viridis*) búvóhelyközpontú menekülési stratégiája/Refuge-based escape behavior in the

- green lizard (*Lacerta viridis*). Állattani közlemények **91**, 127–138.
- López P. and Martín J. (2005a), Female Iberian wall lizards prefer male scents that signal a better cell-mediated immune response. *Biol. Lett.* **1**, 404–406.
- López P. and Martín J. (2005b), Age related differences in lipophilic compounds found in femoral gland secretions of male spiny-footed lizards, *Acanthodactylus erythrurus*. *Z. Naturforsch.* **60c**, 915–920.
- López P. and Martín J. (2005c), Chemical compounds from femoral gland secretions of male Iberian Rock lizards, *Lacerta monticola cyreni*. *Z. Naturforsch.* **60c**, 632–636.
- López P. and Martín J. (2005 d), Intersexual differences in chemical composition of precloacal gland secretions of the amphisbaenian, *Blanus cinereus*. *J. Chem. Ecol.* **31**, 2913–2921.
- López P. and Martín J. (2006), Lipids in the femoral gland secretions of male Schreiber's green lizards, *Lacerta schreiberi*. *Z. Naturforsch.* **61c**, 763–768.
- López P., Muñoz A., and Martín J. (2002), Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. *Behav. Ecol. Sociobiol.* **52**, 342–347.
- López P., Aragón P., and Martín J. (2003), Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflect their mating preference for older males. *Behav. Ecol. Sociobiol.* **55**, 73–79.
- López P., Amo L., and Martín J. (2006), Reliable signaling by chemical cues of male traits and health state in male lizards, *Lacerta monticola*. *J. Chem. Ecol.* **32**, 473–488.
- Louw S., Burger B. V., Le Roux M., and Van Wyk J. H. (2007), Lizard epidermal gland secretions I: Chemical characterization of the femoral gland secretion of the sungazer, *Cordylus giganteus*. *J. Chem. Ecol.* **33**, 1806–1818.
- Mardones P. and Rigotti A. (2004), Cellular mechanisms of vitamin E uptake: relevance in  $\alpha$ -tocopherol metabolism and potential implications for disease. *J. Nutr. Biochem.* **15**, 252–260.
- Martín J. and López P. (2000), Chemoreception, symmetry and mate choice in lizards. *Proc. R. Soc. London B* **267**, 1265–1269.
- Martín J. and López P. (2006a), Links between male quality, male chemical signals, and female mate choice in Iberian rock lizards. *Funct. Ecol.* **20**, 1087–1096.
- Martín J. and López P. (2006b), Interpopulational differences in chemical composition and chemosensory recognition of femoral gland secretions of male lizards *Podarcis hispanica*: implications for sexual isolation in a species complex. *Chemoecology* **16**, 31–38.
- Martín J. and López P. (2006c), Age-related variation in lipophilic chemical compounds from femoral gland secretions of male lizards *Psammodromus algirus*. *Biochem. Syst. Ecol.* **34**, 691–697.
- Martín J. and López P. (2006 d), Vitamin D supplementation increases the attractiveness of males' scent for female Iberian rock lizards. *Proc. R. Soc. London B* **273**, 2619–2624.
- Martín J., Civantos E., Amo L., and López P. (2007a), Chemical ornaments of male lizards *Psammodromus algirus* may reveal their parasite load and health state to females. *Behav. Ecol. Sociobiol.* **62**, 173–179.
- Martín J., Moreira P. L., and López P. (2007b), Status-signalling chemical badges in male Iberian rock lizards. *Funct. Ecol.* **21**, 568–576.
- Mason R. T. (1992), Reptilian pheromones. In: *Biology of the Reptilia*, Vol. 18 (Gans C. and Crews D., eds.). University of Chicago Press, Chicago, pp. 114–228.
- Nettman H. K. and Rykena S. (1984), *Lacerta viridis* (Laurenti, 1768) – Smaragdeidechse. In: *Handbuch der Reptilien und Amphibien Europas*, Vol. 2/1 (Böhme W., ed.). Aula Verlag, Wiesbaden, Germany, pp. 129–180.
- Novotny E. H. and Martin-Neto L. (2002), Effects of humidity and metal ions on the free radicals analysis of peat humus. *Geoderma* **106**, 305–317.
- Olsson M., Madsen T., Nordby J., Wapstra E., Ujvari B., and Wittsell H. (2003), Major histocompatibility complex and mate choice in sand lizards. *Proc. R. Soc. London B (Suppl.)* **270**, 254–256.
- Puky M., Schad P., and Szövényi G. (2005), *Herpetological Atlas of Hungary/Magyarország Herpetologiai Atlasza*. IUCN SSC Hungary, Budapest, Hungary.
- Saladino R., Neri V., Farina A., Crestini C., Nencioni L., and Palamara A. T. (2008), A novel and efficient synthesis of tocopheryl quinones by homogeneous and heterogeneous methyltrioxorhenium/hydrogen peroxide catalytic systems. *Adv. Synth. Catal.* **350**, 321–331.
- Václav R., Prokop P., and Fekiac V. (2007), Expression of breeding coloration in European green lizards (*Lacerta viridis*): variation with morphology and tick infestation. *Can. J. Zool.* **85**, 1199–1206.
- Weldon P. J., Shafagati A., and Wheeler J. W. (1987), Lipids in the gular gland secretion of the American alligator (*Alligator mississippiensis*). *Z. Naturforsch.* **42c**, 1345–1346.
- Weldon P. J., Shafagati A., and Wheeler J. W. (1988), Lipids from the paracloacal glands of the American alligator (*Alligator mississippiensis*). *Lipids* **23**, 727–729.
- Weldon P. J., Flachsbarth B., and Schulz S. (2008), Natural products from the integument of nonavian reptiles. *Nat. Prod. Rep.* **25**, 738–756.