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Space Use Strategies and Nuptial Color in European Green Lizards

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ABSTRACT: The conspicuous colors found in many lizards transfer information about their owner's characteristics that are relevant to mating and social systems. Female European Green Lizards (*Lacerta viridis*) have been shown to prefer males with high ultraviolet (UV) throat reflectance. Additionally, components of throat patch color (such as UV chroma and brightness) have been shown to be condition-dependent and to signal relative head size and health status. In this study, we investigated whether or not different components of male nuptial color and other relevant traits were associated with characteristics of male space use during the reproductive season at two different locations. In Site 1, lizard density was two times higher, territory size was one third as large, and spatial overlap between territories was about half as large as in Site 2. Males at Site 1 showed movement patterns consistent with a mix of territorial and floater individuals, with floaters exhibiting greater throat brightness. Those males at Site 2 moved in a less predictable manner within the study plot, irrespective of their nuptial color. Among territorial males, those of larger head size occupied larger territories but maintained lower brightness and blue chroma. Our results indicate that (1) not all males are territorial; (2) being territorial might have a cost expressed in duller nuptial color; (3) components of nuptial color can signal territory size; and (4) the information content of a multiple signaling system may vary between populations according to the mating system structure present.

Key words: Color signal; *Lacerta viridis*; Multiple signaling system; Sexual selection; Spatial behavior; Territoriality

RELIABLE sexual signals advertise aspects of owner (i.e., genetically determined attributes affecting reproductive success; Zahavi 1977; Iwasa and Pomiankowski 1991). Reliability is ensured through developmental and/or maintenance costs that are not affordable for all individuals (Grafen 1990; Guilford 1995). Color patches have been demonstrated to act as costly honest signals, whether colors are produced by pigments (e.g., red or yellow) or microstructures (e.g., ultraviolet [UV] and blue; Prum 2006). Sexually selected traits can not only act by themselves, but together in a multiple signaling system (Iwasa and Pomiankowski 1994; Johnstone 1995; Candolin 2003), where different characteristics of the owner are signaled by different traits, and all are taken into account when estimating individual quality (Møller and Pomiankowski 1993; Badyaev et al. 2001). Benefits gained by female mate choice can be indirect with better genes passed on to offspring, or direct, providing access to better parental care or more resources through a better territory (Calsbeek and Sinervo 2002a; Stapley and Keogh 2006).

Territoriality is present in numerous taxa, allowing females to choose their reproductive partners based on the quality of the area males occupy (Roithmair 1994). Large territories can signal better fighting ability and risk-taking of the owner (Candolin and Voigt 2001), or can simply be advantageous because of the greater amount of resources available within them (Morse 1980; Kwiatkowski and Sullivan 2002a). Color signals in birds are typically honest signals of territory size and/or other aspects of quality (Keyser and Hill 2000; Pryke et al. 2001). Additionally, pigment-based coloration can affect outcome of female mate choice and male competition and can represent territory size at the same time in a bird species (Griggio et al. 2007). Rapidly changing environments can result in the coexistence of diverse space-use strategies; however, each strategy is adaptive under a different set of conditions. Pigment-based signals can indicate such dynamically changing space-use strategies (Sinervo and Lively 1996). Hence, color signals are not only connected to genetically determined morphological characters, but can also inform conspecifics about owners' current space use and territory attributes.

Many lizard species are ornamented and show sexual dimorphism in a number of chemical (Martin and Lopez 2000), behavioral (Stuart-Smith et al. 2007), and visual (Whiting et al. 2006) traits that all can act as sexually selected signals. Color signals can be correlated with bite force (Huyghe et al. 2009), social status (Olsson et al. 2009), and body condition (Healey and Olsson 2009). Moreover, structural colors can influence mate choice (LeBas and Marshall 2000; Bajer et al. 2010; Griggio et al. 2010) and male competition (Stapley and Whiting 2006; Bajer et al. 2011). The same type of coloration has also been linked to territory size (Keyser and Hill 2000), but its role in sexual selection and possible links to territory characteristics have not been addressed within the same population. Therefore, we investigated whether or not a color trait that affects mate choice and male competition is related to territory attributes, and thus, provides reliable information about owners' space use.

The European Green Lizard (*Lacerta viridis* Laurenti 1768) is a large lacertid species widespread in Central and Eastern Europe, with males developing blue nuptial coloration on their throat patch with a strong UV component (Bajer et al. 2010). We previously demonstrated that UV color affects male reproductive success via female mate choice and male–male competition (Bajer et al. 2010, 2011). When investigating information conveyed by throat patch color, we reported that components of throat coloration are related to femoral pore asymmetry, head and body size, body condition, and parasite load in this species (Molnár et al. 2012, 2013). Considering that the nuptial throat may act as a multiple signaling system in *L. viridis*, UV and other components might also be related to territory size (cf. Calsbeek and Sinervo 2002b). Because *L. viridis* is a territorial species (Rykena et al. 1996; Václav et al. 2007), we were interested in assessing whether different components of male

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throat color or other morphological traits are related to certain aspects of territoriality.

The aim of this study was to reveal the relationship between nuptial throat color, other possible fitness-related traits (e.g., body size, condition, levels of asymmetry, and ectoparasite load), and attributes of male *L. viridis* territories. Our main goal was to detect any possible relationship between territory size and components of nuptial coloration. Additionally, we explored the connections between morphological variables and attributes of territory. To that end, we measured throat color and morphological traits of male European Green Lizards and monitored their movements during the reproductive season at two sites over two years.

MATERIAL AND METHODS

Study Sites

Our study was conducted during the reproductive seasons of 2008 and 2009, from May until the end of July at two different sites. The sites occur within a forest–scrub–grassland near Tápiószentmárton, Hungary (Site 1 studied in 2008 = 0.07 ha, 47°20′23.80″N, 19°47′8.52″E; Site 2 studied in 2009 = 0.19 ha, 47°20′19.31″N, 19°47′7.93″E; datum = WGS84). Although the vegetation of the study areas was similar during the 2 yr, the forests surrounding the study sites differed. Site 1 was surrounded by a plantation of European Black Pines (*Pinus nigra*), whereas Site 2 was bordered by a forest of White Poplars (*Populus alba*). Lizards were repeatedly observed in forested habitat surrounding Site 2, but never in the black pine forest, possibly because the latter habitat lacked appropriate prey, vegetation, or access to direct sunlight needed for thermoregulation. We established a network of 5-m quadrats over each study site, which allowed us to determine the precise locations of male and female lizards observed during the study (±1 cm; LDM 70 Toolcraft laser distance meter).

Field Surveys and Subject Measurements

At both sites, lizards were caught by noosing during the beginning of the mating season, and males' morphological characters and throat color were measured. We marked each lizard individually and released it at the site of capture. All lizards had intact or well-regenerated tails. We applied two levels of individual marking. As a long-term mark (remaining visible throughout the survey period), we clipped the distal edge of ≤4 collar scales. As a short-term but conspicuous mark, an identification number was written with a black permanent marker on the dorsal surface of each subject. The marks did not appear to have detrimental effects on subject behavior or health. Although the short-term mark disappeared after shedding, each subject was easily reidentified using the long-term mark. No unidentified animals were sighted after the first 6 d in 2008, and the first 9 d in 2009; therefore, we presumed we had marked all lizards at both sites and that our ability to detect lizards at each site was similar.

Observations were made from 0830 to 1030 h, following the morning peak in lizard activity. Data for individual subjects were collected only once in a given day so as to sample the population at a sufficiently regular frequency while minimizing disturbance to the lizards. We only conducted fieldwork on days that were appropriate for lizard activity (i.e., air temperature >20°C, and no rain). Observations were made along a path that allowed us to survey each study site in its entirety. Upon observing a known adult lizard, we recorded its position in the grid. We also counted number of females observed on each male's territory. Because of differences in the weather conditions in the 2 yr, data collection was performed across a span of 75 d in 2008, and a span of 59 d in 2009. We obtained data from 18 males and 24 females in 2008 (Site 1), and 22 males and 30 females in 2009 (Site 2). We considered the number of marked individuals required to effectively estimate the adult population size, and divided that value by area of each site to estimate population density.

For each adult male lizard, we recorded snout–vent length (SVL), head height, head width, and head length with digital calipers (±0.01 cm; Mitutoyo, Japan), and body weight (BW) with an analytical balance (±0.01 g; Mettler, Switzerland). To describe head size, we ran a Principal Component Analysis (PCA) on the three head variables. The first PC had an eigenvalue = 2.77 and factor loadings > 0.95, describing 92.4% of the total variation; hence, the component scores were used as a single variable describing head size in the subsequent analyses. We also counted the number of ectoparasites (Acari: *Ixodes* spp.) present on each male subject.

Spectral reflectance of the males' throat patch was measured with an Ocean Optics USB4000 spectrometer, equipped with DT-Mini-2-GS light-source and QR400-7-SR/BX reflection probe with a single end fixed in an RHP1 holder (Ocean Optics Inc., USA). Details on the use of this device are available in Bajer et al. (2010, 2011) and Molnár et al. (2012). Because all three components are informative in *L. viridis* (Václav et al. 2007; Bajer et al. 2010), we characterized throat reflectance using three variables: total brightness ($R_{320-700}$), UV chroma ($R_{320-400}/R_{320-700}$), and blue chroma ($R_{400-490}/R_{320-700}$; Whiting et al. 2006).

Movement Patterns

The mean (±1 SD) number of sightings for an individual male was 4.3 ± 0.4 in 2008 (range = 2–7) and 6.0 ± 0.5 in 2009 (range = 3–9). We entered the coordinates of each subject's position within the study site into Arcview GIS v3.3 software (Environmental System Research Institute, USA), and calculated subject territories using the minimum convex polygon method (Rose 1982; Ribeiro et al. 2009). The degree of overlap between individual males was estimated separately for each of the study sites.

We used two variables to describe movement patterns of male lizards within each population: (1) the total number of sightings during the study period (hereinafter, frequency); and (2) the mean distance between two consecutive sightings (hereinafter, distance). Because the two variables are autocorrelated, we ran a PCA on frequency and distance to derive a single variable that could describe individual movement patterns (PC1: eigenvalue = 1.20, factor loadings = 0.77). As we expected, response variables differed between the sites (PC1: $t_{38} = -10.99$, $P < 0.001$), so we analyzed data from each site separately.

We applied the following method to analyze movement strategies in each year. First, we tested for correlation between frequency and distance, using Pearson or Spearman rank correlation depending on the normality of the variables.

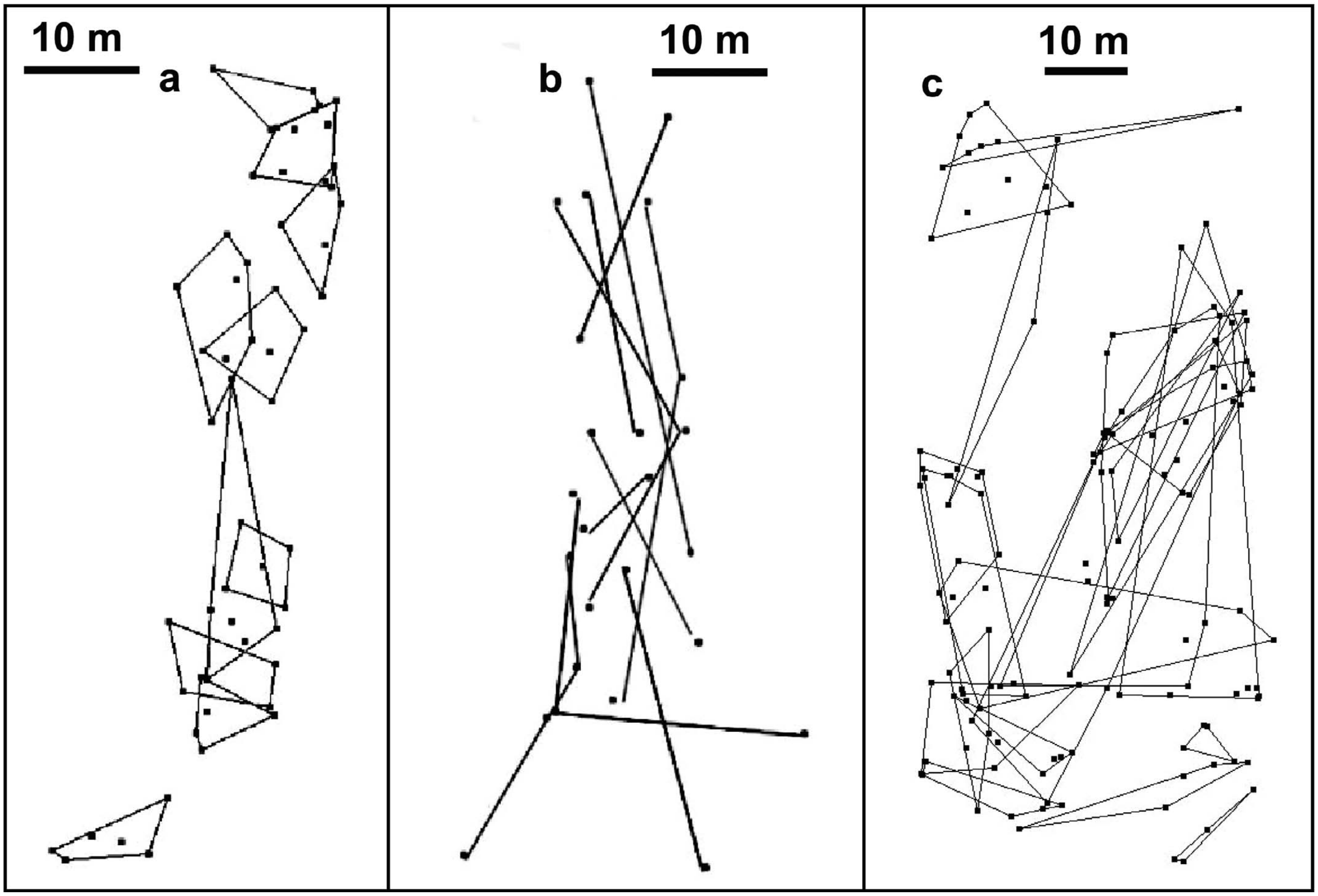

FIG. 1.—Areas occupied by (a) territorial and (b) floater male *Lacerta viridis* in 2008 at Site 1, and (c) nonterritorial males in 2009 at Site 2 within a forest–scrub–grassland near Tápiószentmárton, Hungary. Territorial vs. floater strategies were distinguished based on the distribution of the Principal Component scores describing the strategy (see Fig. 2a). Points represent locations of sightings, connected using the minimum convex polygon method.

If we detected a correlation on a given site, we performed a PCA to collapse the two variables into a single one describing movement patterns. We then determined if the distribution of PC scores indicated discrete strategies, or showed a continuous gradient between extremes, the latter indicating a lack of activity pattern. In the case of discrete distribution (i.e., if strategies were present), we classified the individuals into categories (e.g., floater vs. territorial, or active vs. passive, etc.), based on the direction of the correlation, the individual's position in the distribution, and the number of discrete groups. This process produced a discrete categorical variable to be used in further analyses. In the case of continuous distribution, we analyzed the PC scores themselves. If no correlation was detected, we analyzed the variables separately, using $\log_{10}$ transformations of the original values to achieve normality.

Statistical Analyses

To characterize differences between the two populations, we determined whether density, degree of spatial overlap, and territory size differed between study sites. We applied Chi-square tests to detect any differences in lizard density at the two sites. Because they were nonnormally distributed, we used Mann–Whitney *U*-tests to detect differences in the degree of spatial overlap and in territory size among male lizards.

To further analyze patterns in the data from male lizards at each site, we developed models that incorporated the following explanatory variables: SVL, residual BW and residual head size (residuals were calculated from linear regression against SVL), number of ectoparasites, total brightness, UV chroma, and blue chroma. Following the recommendations of Graham (2003), we used residuals instead of raw variables to avoid problems stemming from correlations and colinearity between SVL, BW, and head size. Based on the correlation structure and distributions, we used one binary response variable for Site 1 (sampled in 2008), and two continuous response variables for Site 2 (2009). The binary variable was analyzed with logistic regression using a logit link, as implemented by PROC GENMOD in SAS v9.1 (SAS Institute Inc., USA). Territory size in 2008 and frequency and distance in 2009 showed normal distributions (Kolmogorov–Smirnov normality test; all $P = 0.20$); in contrast, values for territory size in 2009 were log-transformed in order to achieve normality. All four variables were analyzed using General Linear Models (GLM), whereas negative binomial models (Generalized Linear Models; GLZ) were used to identify possible predictors of the number of females seen in any given male's territory (O'Hara and Kotze 2010). Analyses considering territory size and number of female sightings in 2008 were performed on territorial males only, because these

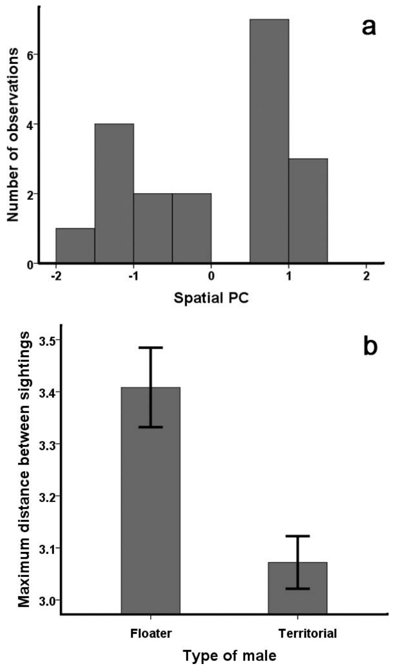

FIG. 2.—(a) Distribution of Principal Component scores describing space use strategy based on a negative correlation between frequency of observations and mean distance between subsequent observations (low numbers = floater strategy; high numbers = territorial strategy) for male *Lacerta viridis* observed in 2008 at Site 1 within a forest–scrub–grassland near Tápiószentmárton, Hungary. (b) Mean values (±1 SE) for the maximum distance (cm) between sightings of territorial vs. floater males.

variables could not be calculated for most of the floater individuals on account of a low sample size. The GLMs and GLZs were performed using SPSS v19 (SPSS Inc., USA). In all the GLMs, GLZs and in the logistic regression, we applied a backward stepwise model selection ($\alpha < 0.05$). We note that, of the options available for model selection, we chose those having conservative criteria (Murtaugh 2009).

RESULTS

2008: Site 1

The estimated population density was 609 lizards/ha for all adults and 261 lizards/ha for males, while the mean male territory size for males was 72.2 m^2 with an estimated average 31.5% spatial overlap. Because neither frequency nor distance met the assumptions of normality (Kolmogorov–Smirnov test; $P \leq 0.03$), we applied a Spearman rank correlation and found a strong negative correlation between frequency and distance ($r = -0.78$, $P < 0.001$, $n = 18$). The PCA conducted with these variables resulted in one PC with an eigenvalue = 1.82 and factor loadings with opposite direction (frequency = 0.953; distance = −0.953), describing 90.8% of the original variation. The negative correlation indicated the presence of different strategies: high frequency and short distance between observations (i.e., territorial) vs. low frequency and long distance between observations (i.e., floater). The distributions of individual spatial movements into different PC score groups (Fig. 1a vs. 1b) and of the PC scores themselves (Fig. 2a) also support the existence of discrete strategies. To exclude the possibility that these patterns are simple artifacts of different detectability of different individuals, we also compared the maximum distance between sightings of territorial and floater males and found that the latter had a 10% larger average maximum distance despite the fewer observations ($F_{1,17} = 14.0$, $P = 0.002$; Fig. 2b).

The logistic regression revealed that the space use strategy in 2008 was related to throat brightness (Table 1a), with territorial males having duller throats than floater males (Fig. 3). Territory size was related to throat brightness, throat blue chroma, and relative head size (GLM; Table 1b), indicating that male lizards holding larger territories had lower throat brightness (Fig. 4a) and blue chroma (Fig. 4b), and larger heads (Fig. 4c), than those defending smaller areas. The number of observed females within the territory of each male showed no relationship with any of the explanatory variables (Table 1c).

2009: Site 2

The estimated population density was 271 lizards/ha for all adults and 115 lizards/ha for males and the mean territory size was 198 m^2 with an estimated mean overlap of 56%. Whereas males at Site 1 occurred at a higher density compared with Site 2 ($\chi^2 = 67.56$, $P < 0.001$), the mean territory size for males at Site 2 was greater ($Z = -4.98$, $P < 0.001$). Considering only those male subjects having four or more sightings (i.e., territorial males from Site 1 and all males from Site 2), lizards at Site 2 defended territories that were approximately three times larger than those at Site 1 ($F_{1,33} = 4.44$, $P = 0.04$; Fig. 5).

For male lizards at Site 2, we did not detect any relationships between any of the predictor variables and frequency of observations, distance moved between observations, male territory size, or the number of females within

TABLE 1.—Logistic regressions illustrating the relationships between measured features of male *Lacerta viridis* at Site 1 (2008) and (a) space use strategy (i.e., territorial vs. floater), (b) territory size, and (c) the number of female sightings of territorial males, based on observations made in 2008 at Site 1 within a forest–scrub–grassland near Tápiószentmárton, Hungary. We applied a backward stepwise model selection in both cases. Nonsignificant effects are shown as seen before removal. Significant effects are in bold font.

	Space use strategy		Territory size			Female sightings	
Effect[a]	χ^2	*P*	*F*	df	*P*	*F*	*P*
SVL (mm)	2.83	0.09	0.29	1,1	0.68	0.01	0.90
Residual head size	2.94	0.09	**21.66**	**1,5**	**<0.01**	0.28	0.59
Residual BW (g)	0.04	0.83	2.01	1,4	0.23	0.68	0.40
LogPar	2.41	0.12	3.96	1,3	0.14	0.04	0.84
Total brightness (R300-700)	**3.97**	**0.04**	**17.54**	**1,5**	**<0.01**	0.18	0.66
UV chroma (R400-490/R300-700)	1.19	0.27	5.22	1,2	0.15	0.78	0.37
Blue chroma (R320-400/R300-700)	1.08	0.29	**34.49**	**1,5**	**<0.01**	0.02	0.87

[a] SVL = snout-vent length; BW = body weight; LogPar = the log-transformed number of ectoparasites; UV = ultraviolet.

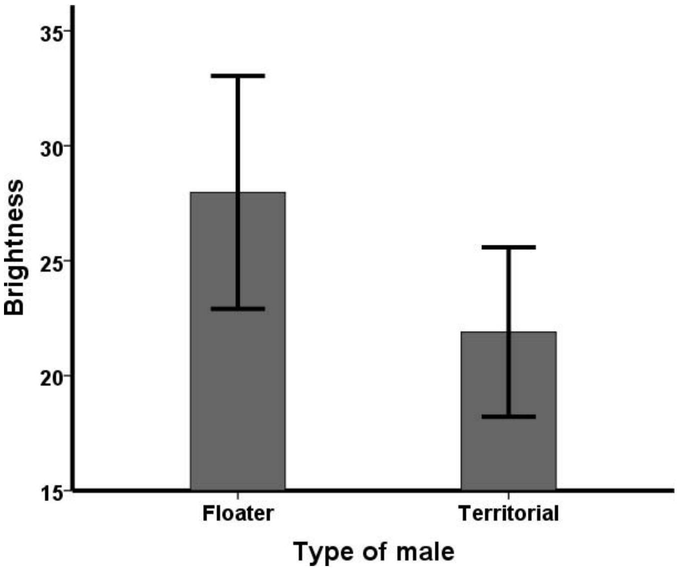

FIG. 3.—Mean values (±1 SE) for throat brightness (% reflectance) of territorial vs. floater male *Lacerta viridis* observed in 2008 at Site 1 within a forest–scrub–grassland near Tápiószentmárton, Hungary.

a territory (Table 2). Specifically, frequency of, and distance between, observations were not correlated ($r_{22} = 0.22$, $P = 0.37$). These results indicate that a large proportion of male *L. viridis* at Site 2 moved more randomly than at the other site and exhibited a less rigid territorial structure (Fig. 1c).

DISCUSSION

Our results show that sexual coloration conveys information about the owner's space-use strategies, but that the information content is context-dependent. We described three spatial strategies (floater, territorial, random mover) in a species previously considered to be only territorial (Rykena et al. 1996; Václav et al. 2007). Floaters had brighter throats than territorial individuals, and territorial males with larger heads and duller color occupied larger areas. We suggest that coloration can play a significant role in conveying information about spatial behavior and territory size.

Whereas lizards at Site 1 showed two alternative spatial strategies (territorial or floater), those at Site 2 moved more randomly. These differences might be attributable to differences in individual detectability within and between the sites. The patterns reported here are likely valid, however, because (1) all individuals were first observed within a small timeframe; (2) floaters had 10% larger maximum distance between sightings than territorial males despite their lower number of sightings; and (3) territories of males from Site 2 were approximately three times larger than those from Site 1. Diverse space-use strategies can indicate either ontogenetic changes (Calsbeek and Sinervo 2002b; Manteuffel and Eiblmaier 2008) or actual differences in sexual strategies (Sinervo and Lively 1996; Kwiatkowski and Sullivan 2002b). Given that lizards show indeterminate growth, if spatial strategies were connected to ontogeny, we would expect a correlation between SVL and movement strategy and/or territory size. We reject this explanation, however, because there was no relationship between size and movement patterns.

Populations also differed in density and average territory size. One explanation for different densities could be the different surroundings of the sites, namely the stands of Black Pines in Site 1, and that of White Poplars at Site 2. During the period of the study, no animals were observed in the pine plantation, possibly on account of the insufficient amount of available sunlight, food resources or shelters. In contrast, individuals of both sexes were regularly observed in areas of White Poplar, which probably provide more resources than areas planted in Black Pine. Therefore, we feel confident that the population in Site 2 had a larger area to occupy than that in Site 1.

Mating systems (e.g., territorial vs. floater, promiscuous vs. lekking) have been demonstrated to show diversity according to population density (Kwiatkowski and Sullivan 2002b), dispersion of prey (van Rensburg and Mouton 2009), or density of predators (Manteuffel and Eiblmaier 2008). Our observations regarding different social systems and space use strategies (territorial, floater, and random mover) at different sites indicate that territorial behavior is context-dependent in *L. viridis*. Although our sampling design does not allow us to establish causality, we suggest that increasing male density exaggerates social tension, and the loose, largely overlapping space use can shift into strict strategies. Our results indicate that the spatial pattern of particular species cannot be generalized across populations having different environmental or habitat constraints.

Male *L viridis* that we described as floaters had brighter throat-patch color than territorial males. Throat coloration has already been shown to be a multiple signaling system in this species (Bajer et al. 2010, 2011; Molnár et al. 2012, 2013), and our results indicate that it might also convey information about owners' space use. There are two possible explanations for the relationship between spatial behavior and throat brightness in this species: (1) through the cost

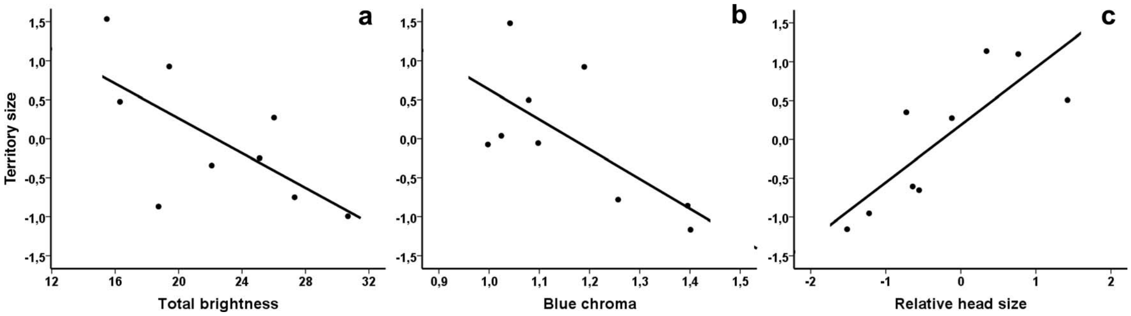

FIG. 4.—Correlations between territory size and total brightness (% reflectance; a), blue chroma (b), and relative head size (c) of territorial male *Lacerta viridis* observed in 2008 at Site 1 within a forest–scrub–grassland near Tápiószentmárton, Hungary. Territory size is characterized by residuals of the final model.

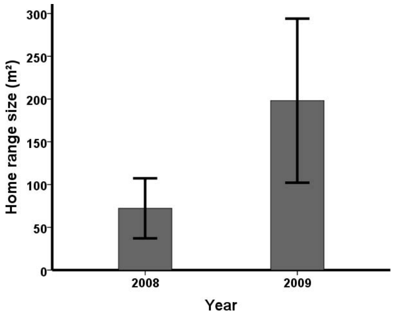

FIG. 5.—Mean values (±1 SE) for territory sizes of territorial males from 2008, Site 1, and all males from 2009, Site 2 within a forest–scrub–grassland near Tápiószentmárton, Hungary (i.e., males with four or more sightings). Territory size is characterized by residuals of the final model.

associated with territory defense, or (2) as a result of territorial individuals acquiring less energy. If territorial males invest more energy into agonistic interactions or suffer from greater predation risk, they might have less ability to afford to develop conspicuous bright color, unlike floaters (e.g., Diaz-Uriarte 1999; Whiting et al. 2006). On the other hand, if we assume floaters are of better quality with more energy to invest into color, it raises the possibility that males considered to be territorial are rather just males occupying smaller territories without any territorial interaction (Main and Bull 2000). Our prior analyses that included data from male lizards over several years revealed an association between brighter throat color and low ecto- and endoparasite load and larger body size (Molnár et al. 2012, 2013), supporting the second hypothesis. Our observations of male lizards initiating fights during the mating season, coupled with a time and energy cost associated with bright nuptial coloration (Bajer et al. 2012), support the hypothesis that territorial males possess duller coloration on account of the costs of territorial activity.

TABLE 2.—Results of logistic regressions illustrating the relationships between measured features of male *Lacerta viridis* at Site 2 within a forest–scrub–grassland near Tápiószentmárton, Hungary (2009) and (a) frequency of observations, (b) mean distance between subsequent observations, (c) territory size, and (d) number of female sightings. We applied a backward stepwise model selection in all cases. Nonsignificant effects are shown as seen before removal.

	Statistical Results		
Effect[a]	*F*	df	*P*
(a) Frequency of observations			
SVL (mm)	0.12	1,14	0.72
Residual head size	1.70	1,18	0.20
Residual BW (g)	0.49	1,19	0.49
LogPar	1.45	1,17	0.24
Total brightness (R300-700)	2.32	1,20	0.14
UV chroma (R400-490/R300-700)	0.19	1,15	0.66
Blue chroma (R320-400/R300-700)	0.87	1,16	0.36
(b) Mean distance			
SVL (mm)	1.11	1,19	0.30
Residual head size	<0.01	1,15	0.93
Residual BW (g)	<0.01	1,14	0.99
LogPar	2.48	1,18	0.08
Total brightness (R300-700)	2.73	1,20	0.11
UV chroma (R400-490/R300-700)	0.30	1,17	0.59
Blue chroma (R320-400/R300-700)	0.03	1,16	0.86
(c) Territory size			
SVL (mm)	0.32	1,19	0.57
Residual head size	0.25	1,17	0.61
Residual BW (g)	0.02	1,15	0.88
LogPar	0.47	1,18	0.49
Total brightness (R300-700)	0.50	1,20	0.48
UV chroma (R400-490/R300-700)	0.18	1,16	0.67
Blue chroma (R320-400/R300-700)	<0.01	1,14	0.93
	χ^2		*P*
(d) Female sightings			
SVL (mm)	<0.01		0.95
Residual head size	0.29		0.58
Residual BW (g)	0.72		0.39
LogPar	0.46		0.49
Total brightness (R300-700)	1.79		0.18
UV chroma (R400-490/R300-700)	0.10		0.74
Blue chroma (R320-400/R300-700)	0.01		0.91

[a] SVL = snout-vent length; BW = body weight; LogPar = the log-transformed number of ectoparasites; UV = ultraviolet.

When examining possible determinants of territory size within territorial lizards seen at Site 1, we found negative correlations with throat total brightness and blue chroma, and a positive correlation with head size. The negative correlations with color traits are explicable on the same grounds discussed above. Males with larger heads have been demonstrated to exhibit a larger bite-force (Husak et al. 2006), social dominance (Lopez et al. 2002), greater mating success (Bull and Pamula 1996), and a greater likelihood of winning male–male combats (Ribeiro et al. 2009). Therefore, male lizards with larger heads might also be more successful in acquiring larger territories. The fact that males with relatively larger heads and larger territories had duller throat color further indicates that duller color is a cost of territoriality rather than sign of lower available energy. At Site 2, lizards moved more randomly, and their territory size was not related to any of the variables considered, indicating that space use in this context was not constrained by other individual attributes.

Throat patch color was only informative about movement patterns when male *L. viridis* exhibited a territorial strategy, but not when space use was random. We suggest that information content of a sexual signal can vary according to mating systems, providing accurate information about owners' individual characteristics.

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