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Does reproductive mode affect sexually-selected coloration? Evaluating UV–blue spots in parthenogenetic and bisexual lizards of the genus *Darevskia*

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Abstract

Sexual selection often leads to evolution of conspicuous signals, raising the chances of attracting not only potential mates, but also predators. In lacertid lizards, ultraviolet (UV)–blue spots on flanks and shoulders represent such a trait. Some level of correlation between male and female ornamentation is also known to exist. Therefore, the phenotype of females may change in the absence of sexual selection. We tested this hypothesis on a complex of parthenogenetic and bisexual lizards of the genus *Darevskia*. We evaluated area, counts, and chromatic properties (UV opponency, saturation) of UV–blue spots and compared the values between the clones and their bisexual progenitor species. We found a fair heterogeneity between the parthenogenetic species, but no general tendency toward higher crypsis or conspicuousness. Values of the parthenogens were not significantly different from the values of sexual females. A possible explanation is that the changes in selective forces associated with parthenogenetic reproduction are too small to affect the resulting pattern of selective pressures on the studied traits, or that the phenotypes of the parthenogens result from the unique combination of parental genomes and are conserved by clonal reproduction.

Key words: clonal reproduction, coloration, reptiles, sexual selection, visual modeling

Sexual selection frequently leads to the evolution of sexually dimorphic traits, with males being the more conspicuous sex (Darwin 1871; Andersson 1994). These traits may indicate good health condition or social dominance and thus increase the male's mating success (Hamilton and Zuk 1982; Møller 1988; Milinski and Bakker 1990; Kodric-Brown 1993). In reptiles, and lizards, in particular, a whole range of colorful ornaments evolved, many of them having a role in intraspecific/social signaling (Sinervo and Lively 1996; Nicholson et al. 2007; Pérez I de Lanuza et al. 2014). As the visual system of diurnal reptiles (but also birds, for instance) is tetrachromatic with ultraviolet-sensitive (UVS) cones, it is natural that UV coloration takes part in their signaling too (Fleishman et al. 1993;

Loew et al. 2002; Stevens and Cuthill 2007; Mullen and Pohland 2008; Pérez I de Lanuza et al. 2013; Marshall and Stevens 2014; Pérez I de Lanuza and Font 2014). UV ornamentation is frequently involved in sexual selection in lizards (Whiting et al. 2006; Pérez I de Lanuza et al. 2013; Lisboa et al. 2017). A number of lacertid species have UV–blue spots on their throats, shoulders, flanks, or bellies, which are more prominent in males than females (e.g., *Gallotia galloti* (Molina-Borja et al. 2006), *Timon lepidus* (Font et al. 2009), *Podarcis* sp. (Pérez I de Lanuza and Font 2010; Pérez I de Lanuza et al. 2014; Names et al. 2019)). The UV coloration in males also positively correlates with their fighting ability or mating success, as was reported, for example, in the European green lizard, *Lacerta*

viridis (Bajer et al. 2011; Molnár et al. 2012), sand lizard, *L. agilis* (Olsson et al. 2011), Schreiber's green lizard, *L. schreiberi* (Martín and López 2009), or common wall lizard, *Podarcis muralis* (Pérez I de Lanuza et al. 2014; MacGregor et al. 2017).

In our study, we focused on UV–blue spots on shoulders and outer ventral scales (henceforth OVS) in Caucasian rock lizards of the genus *Darevskia* (Lacertidae) (Arribas 2012; Abramjan et al. 2015). The genus is remarkable for comprising 7 obligatory parthenogenetic diploid species, which arose from interspecific hybridization of at least 4 bisexual species, 2 being paternal, and 2 being maternal ancestors (Moritz et al. 1992; Freitas et al. 2016, 2019; Tarkhnishvili et al. 2017). *Darevskia* lizards cluster into 3 main groups, with paternal species belonging to 1 group and maternal species to another (Murphy et al. 2000). As the parthenogens lack males, we decided to explore whether the absence of sexual selection affects their UV–blue coloration. First, the conspicuous traits may positively correlate between the sexes due to shared genetic basis (Lande 1980; Potti and Canal 2011). Furthermore, in mutual mate choice, not only females, but also males actively select more attractive partners (Jones and Hunter 1993; Amundsen 2000). Therefore, we may presume that in the absence of males, other evolutionary pressures can take precedence, which might subsequently affect females' coloration. Various scenarios can be imagined. Predation can select for better crypsis (Stuart-Fox et al. 2003; Husak et al. 2006; Marshall et al. 2015). By contrast, competition over resources may enhance female ornamentation (Jenssen et al. 2000; LeBas 2006; Pryke 2007; Hegyi et al. 2008). This may be possible in the parthenogenetic *Darevskia* lizards, as they occur in high densities and their social interactions are more frequent than in sexual species (Darevsky 1967). Yet, their interactions are usually peaceful and their home ranges overlap more than in females of bisexual species (Galoyan 2013a). On the contrary, increased aggressiveness among the clonal females was reported from hybrid zones, where they mate with males of related bisexual species and compete for their attention (Danielyan et al. 2008; Galoyan 2013a, 2013b; Spangenberg et al. 2017).

Male appearance is rather costly and can reduce fitness due to physiological and behavioral causes (Swierk and Langkilde 2013). Higher conspicuousness also leads to better detectability. In many lacertids, including *Darevskia* sp., males copulate with multiple females, selecting the largest ones, likely in order to increase paternity chances (Carretero et al. 2018). During the mating, the male holds the female for some time, biting her inguinal region or thigh and leaving noticeable jaw marks on her body (Darevsky 1967). Thus, being easily detected and frequently mated can induce a considerable reproductive cost on females, for example, by increasing risk of predation due to reduced mobility, risk of injuries, or sexual transmission of pathogens (Le Galliard et al. 2005; White et al. 2011). Parthenogenetic females would be spared sexual conflict, so there would be no need for decreased conspicuousness. In spite of this, copulation between parthenogenetic *Darevskia armeniaca* or *D. unisexualis* and bisexual *D. valentini* is a common phenomenon in mixed communities. Such hybridizations usually result in sterile triploid offspring (Darevsky 1966), but may sporadically lead to the return to bisexuality via higher level of ploidy in the process of reticulate evolution (Danielyan et al. 2008; Carretero et al. 2018).

To sum up, there are multiple evolutionary pressures which can potentially affect the ornamentation in parthenogenetic females. In order to find out whether the conspicuousness of UV–blue coloration differs between sexual and parthenogenetic species, we examined the quantity and color properties of UV–blue spots in 4

parthenogens: (*D. armeniaca*, *D. dahli*, *D. rostombekowi*, and *D. unisexualis*) and their respective paternal (*D. portschinskii*, *D. valentini*) and maternal (*D. raddei raddei*/*D. raddei nairensis*, *D. mixta*) and 1 unrelated (*D. caucasica*) species.

Materials and Methods

The material comprised 326 lizards of 9 species. One species, *D. caucasica*, is unrelated to the parthenogens, but belongs to the same phylogenetic group as the maternal species *D. raddei* and *D. mixta* (Murphy et al. 2000). The lizards were captured in the wild in Armenia during their breeding season from May to July (2010–2019). Lizards from Georgia, also captured in the wild during the same period, were accessed at a private breeder. Shortly after acquiring the lizards, we recorded their snout-vent length (SVL) using a digital caliper with 0.01 mm precision and took digital images for further color analyses. Sample sizes are given in Table 1. For populations, see Appendix 1. For better precision, we decided to discriminate between *D. raddei nairensis* and *D. raddei raddei* in this study. Although conspecific, each of the subspecies contributed to formation of a distinct parthenogen; *D. unisexualis* is related to *D. r. nairensis* (Freitas et al. 2016), whereas *D. rostombekowi* is probably related to *D. r. raddei* (Fu et al. 2000). Unfortunately, no live *D. mixta*, the maternal ancestor of *D. armeniaca* and *D. dahli*, was available to us. We could examine only ethanol-fixed museum specimens, whose coloration was partially faded. We excluded them from the statistical models, but we present the data in the results.

Image acquisition and processing

We focused on both quantitative and chromatic characteristics of UV–blue spots in 2 body regions—the row of OVS and the shoulder. In OVS, we assessed the quantitative parameters ($n = 326$): area of the UV–blue coloration and number of UV–blue spots. We scanned each lizard together with a millimeter scale with an Epson GT-S640 scanner at 600 dpi resolution. We cut out both left and right rows of OVS in Adobe Photoshop CS6 and calculated the area of the blue color (corresponding to UV–blue) for each row with Barvocuc software (Rádlová et al. 2016) (Figure 1). The hue angle for blue was set to 175°–275° and the upper threshold for gray (nonsaturated colors) to 8%. Blue areas from left and right flank were averaged. Absolute values in square millimeter were used for statistical modeling. In the graphs, we present percentage of UV–blue per row of OVS, as it is more intuitive. The number of UV–blue spots was counted manually for each side of a lizard. Outputs from Barvocuc

Table 1. Sample sizes used in this study

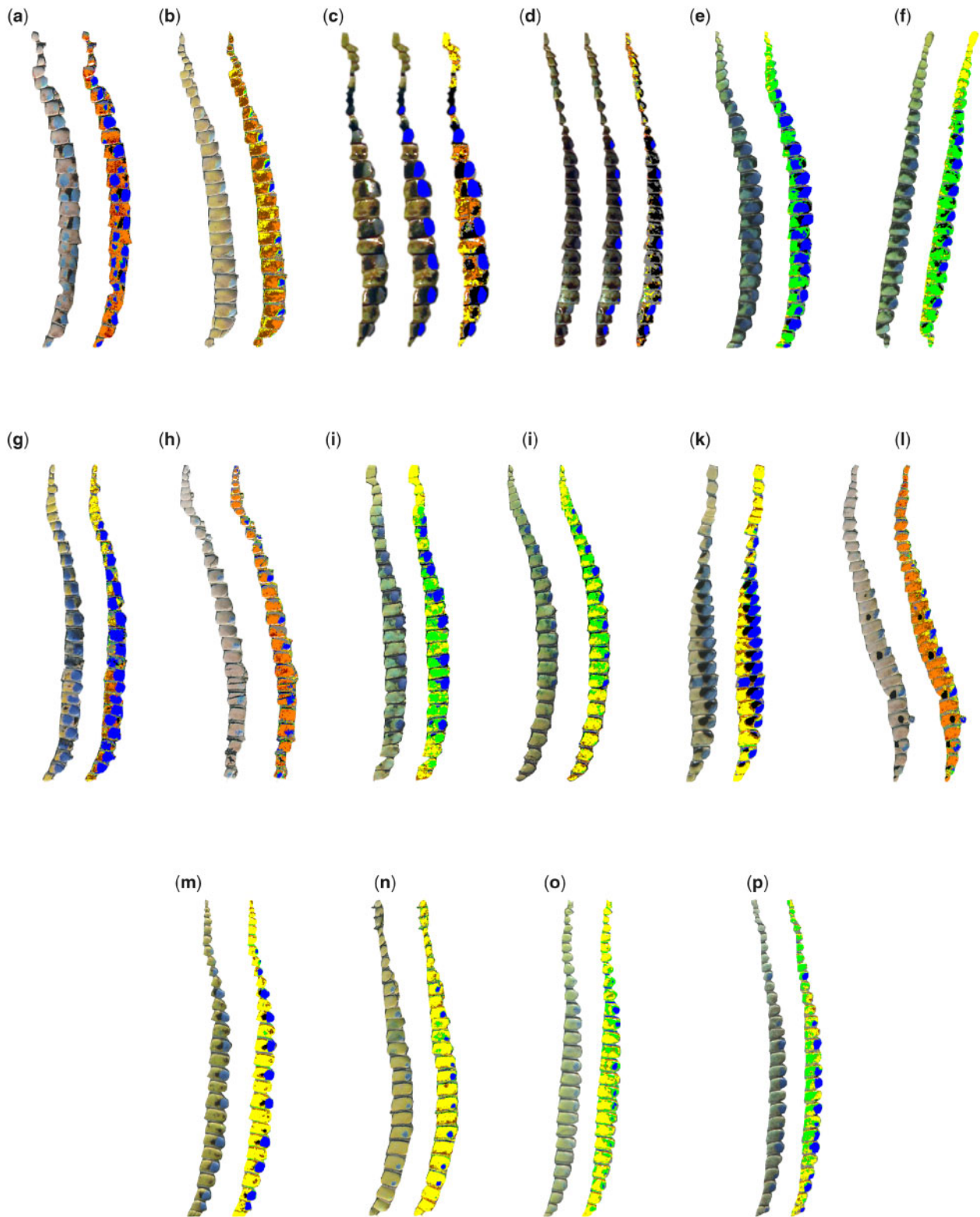| Species	Males	Females
Bisexual		
Darevskia caucasica	14	17
Darevskia mixta[a]	14	24
Darevskia raddei nairensis	16	12
Darevskia raddei raddei	20	10
Darevskia portschinskii	21	21
Darevskia valentini	12	15
Parthenogenetic		
Darevskia armeniaca		76
Darevskia dahli		24
Darevskia rostombekowi		15
Darevskia unisexualis		15

[a] Ethanol-fixed specimens.

Figure 1. Examples of OVS rows used for the analysis of quantitative parameters of the UV–blue spots. Each pair shows the original scan (left) and the output from Barvocuc software (right). In *D. mixta*, the middle row shows the digitally reconstructed pattern; (**a**) *D. caucasica* male, (**b**) *D. caucasica* female, (**c**) *D. mixta* male, (**d**) *D. mixta* female, (**e**) *D. r. nairensis* male, (**f**) *D. r. nairensis* female, (**g**) *D. portschinskii* male, (**h**) *D. portschinskii* female, (**i**) *D. r. raddei* male, (**j**) *D. r. raddei* female, (**k**) *D. valentini* male, (**l**) *D. valentini* female, (**m**) *D. armeniaca*, (**n**) *D. dahli*, (**o**) *D. rostombekowi*, (**p**) *D. unisexualis*. (a–l) Bisexual species, (m–o) partheno-genetic species. Scale not preserved.

were used for counting and the original scans as a control. Counts from both sides were summed for each lizard.

The museum specimens of *D. mixta* were photographed on a millimeter paper with a Nikon E4500 digital camera. Because their UV–blue spots were partially faded, they had to be manually selected and highlighted in Adobe Photoshop, to make them "visible" to Barvocuc software. The measurements were compared with data retrieved from photographs of live *D. mixta*, kindly provided by D. Tarkhnishvili. In order to make the estimation as objective as possible, the procedure was repeated twice by two of the authors (A.A. and D.F.). Unfortunately, the same result could not be obtained repeatedly—the difference between live and fixed specimens was significant in 2 out of 4 tests. The discrepancy was likely caused by high variance in coloration between live and fixed individuals and by varying angles and framings in each set of photographs. Therefore, we excluded these data from the statistical models, but we present the best estimates we could achieve in the results.

Chromatic parameters were measured for both OVS and shoulder spots and included 1) the UV opponency, which we use as a measure of dominance of the UV color and 2) saturation (chroma). For this purpose, we used UV photography and Multispectral Image Calibration and Analysis (MICA) Toolbox v2 (van den Berg et al. 2020), a freely available plug-in operating on ImageJ platform (Schneider et al. 2012). Our multispectral photo equipment was available only during one part of our study, therefore a limited number of lizards could be examined photographically. Besides, some of them had only one or no UV–blue spots on their flanks or shoulders. Therefore, only smaller subsets of individuals could be used for saturation and UV opponency measurements (OVS subset $n = 91$; shoulder spot subset $n = 70$; see Appendix 2 for details).

Animals with at least 3 UV–blue spots on OVS or 1 UV–blue spot on shoulder, respectively, were selected. Each lizard was photographed from its lateral side through UV/IR cut filter, transmitting visible light 400–700 nm, and then UV pass Baader U-Venus filter, transmitting 300–400 nm (Figure 2). We used a Samsung NX1000 camera, adapted for UV photography according to the instructions by J. Troscianko available at https://www.jolyon.co.uk/2014/07/full-spectrum-nx1000/, and a 35 mm Novoflex Noflexar lens. Lizards were placed 16 cm away from the lens and illuminated by Iwasaki ColorEyeArc bulb with its UV blocking coating removed.

The lamp was set 20 cm above the lens. One-millimeter thick white PTFE (Teflon) plates, obtained from a local manufacturer (Techseal, www.techseal.cz), were put around the lizard to eliminate undesirable shadows. Photographs were calibrated against a white PTFE tape having flat 99% reflectance from 300 to 700 nm, which was checked by spectrophotometer against white WS-1 diffuse reflectance standard. The photographs were taken at a setting ISO400, F/16, and further processed with the MICA toolbox according to the methodology of Troscianko and Stevens (2015) and van den Berg et al. (2020).

The 3 largest UV–blue spots were selected on each lizard's OVS and treated together as 1 region of interest. As for the shoulder spots, we always selected the largest. For visual modeling, we used the photoreceptor data for *P. muralis*, cone abundance ratio UVS:SWS:MWS:LWS 1:2:5:9, Weber fraction 0.05 (Martin et al. 2015). Each multispectral stack was then converted to receptor noise limited (RNL) XYZ chromaticity system. XYZ stands for the 3 axes corresponding to opponent channels in a tetrachromat's vision. X, Y, and Z axes represent "red-green" (LW:MW), "yellow-blue" ([LW + MW]:SW), and (LW + MW + SW):UV opponency, respectively. Each color is therefore described by 3 coordinates in the RNL XYZ chromaticity color space and the distance between any 2 points is in units of "just noticeable distances" (jnds) (van den Berg et al. 2020). UV opponency is expressed in Z-axis values with UV dominance increasing in the positive direction. Saturation of the spot is expressed as the mean of Euclidean distances of each pixel's color to the achromatic origin of the color space.

Statistical analysis

We checked the data for normality and applied log transformation where needed (UV–blue area, spot saturation). In statistical models involving log-transformed response variables, we also used log-transformed SVL to allow interpretation in terms of allometry. A dataset comprising 83 males, 75 sexual, and 130 parthenogenetic females was used for statistical models analyzing UV–blue area and spot count (both for OVS). UV opponency and saturation were analyzed on smaller subsets (Appendix 2).

Calculations were performed with R v3.6.2 ("nlme" package) (R Core Team 2018) and Statistica 8 software (StatSoft 2007). First, we tested for differences between males and females in bisexual
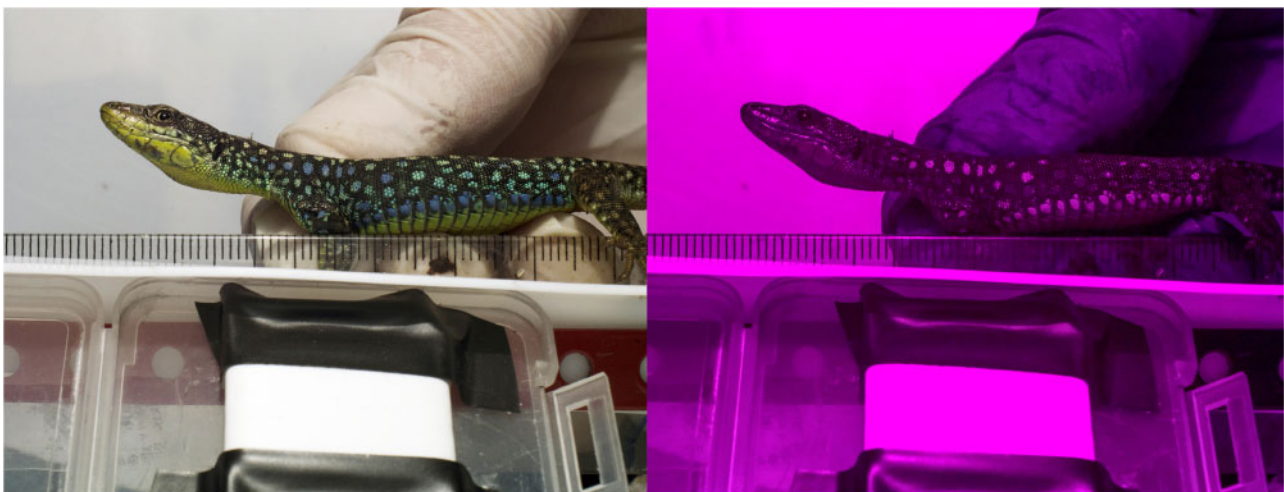

Figure 2. Example of photos taken in the visible and UV spectra, used for multispectral image analysis of saturation and UV opponency. The photo shows a male *D. r. nairensis*.
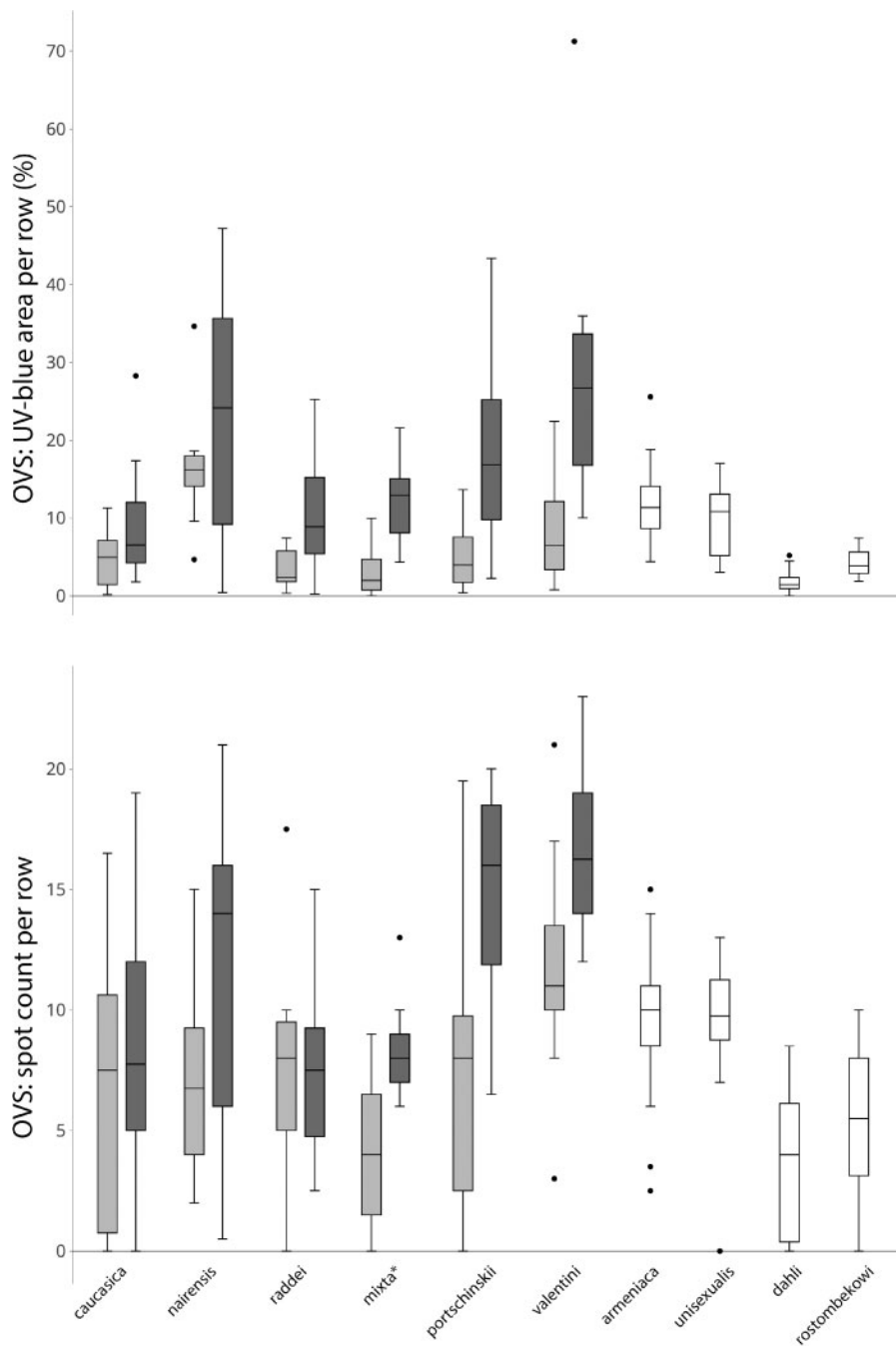
Figure 3. Quantitative parameters of OVS spots by species and sex. Dark gray = males, light gray = females, white = parthenogens. Box plots: middle line = median, box = 1st–3rd quartile, whiskers = nonoutlier range, dots = outliers. *Values of *D. mixta* are based on measurements of ethanol-fixed individuals.

species. We ran linear models (LMs) for the following response variables: UV–blue area ($n = 158$), OVS UV opponency ($n = 46$), OVS saturation ($n = 46$), shoulder UV opponency ($n = 33$), and shoulder saturation ($n = 33$). Sex, species, SVL, and their interactions (sex × species, sex × SVL, species × SVL) were set as predictors. We also checked for the effect of outliers using Cook's distances and reran the models without the selected observations. The results were unaffected. The full model was further reduced according to AIC (command "step"). In the case of spot count ($n = 158$), we used generalized linear model (GLM) with quasipoisson distribution and

chi-square test. The order of the predictors was the same as in the LM.

Next, we compared differences between all 3 "sex categories" (males, sexual females, and parthenogenetic females) in quantitative as well as chromatic parameters. We used generalized least squares (GLSs) method for analyzing UV–blue area ($n = 288$), OVS UV opponency ($n = 91$), OVS saturation ($n = 91$), shoulder UV opponency ($n = 70$), and shoulder saturation ($n = 70$). This method enables analyzing correlated data, in our case treating species as independent observations and individual measurements within each
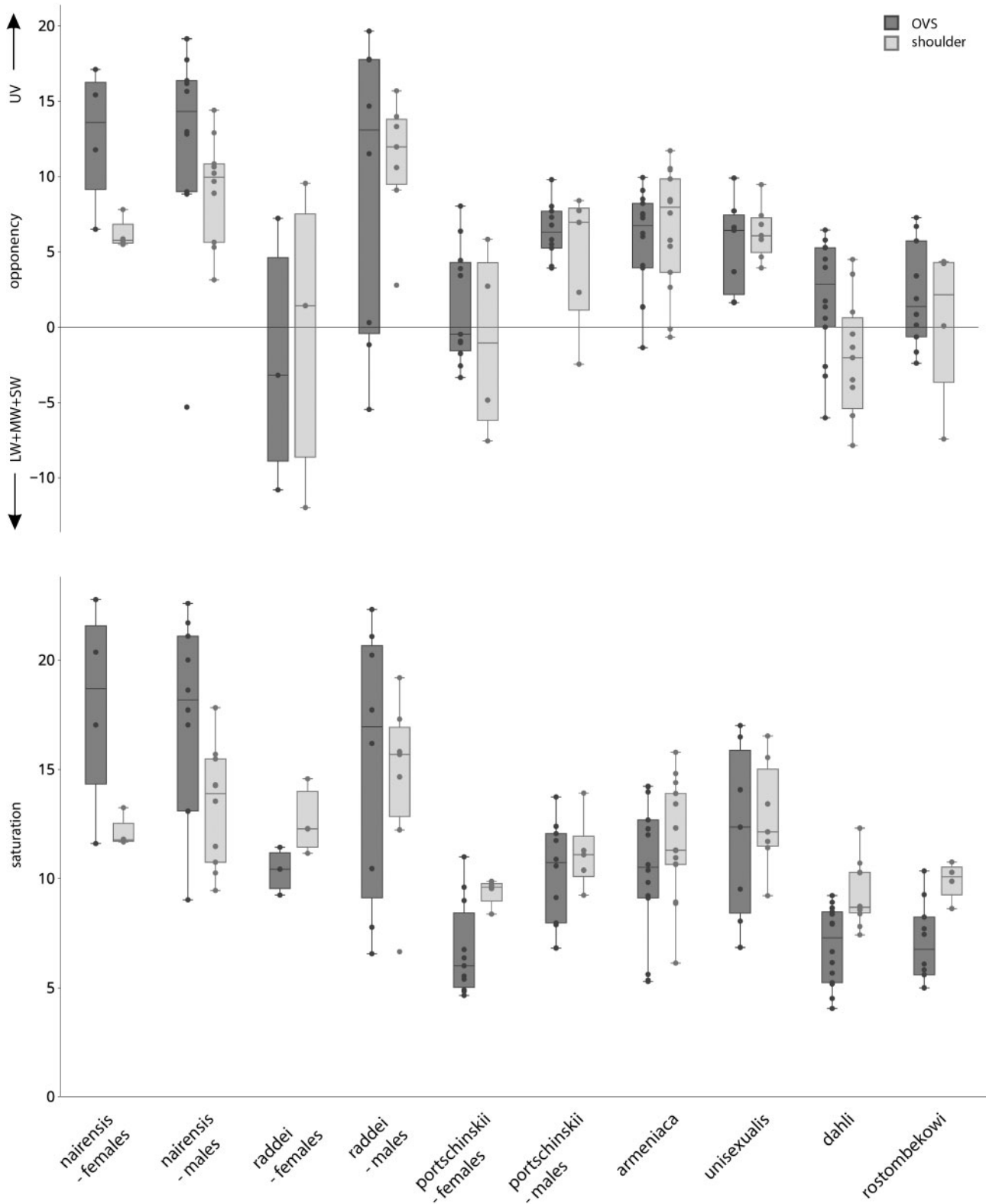
Figure 4. Chromatic parameters of OVS and shoulder spots by species and sex. Middle line = median, box = 1st–3rd quartile, whiskers = nonoutlier range, dots = raw data. *Y*-axis in the UV opponency graph represents the (LW + MW + SW):UV color opponency. Both *Y*-axes are in units of "just noticeable differences" (jnds).

Table 2. ANOVA/ANODEV results for the quantitative and chromatic parameters of the UV–blue spots

	OVS: UV–blue area			OVS: Spot count				
	LM			GLM				
	df	F	P	df	Deviance	Resid. df	Desid. dev	P
Residuals	142			157			1296.64	
Sex	1	43.261	**<0.001**	1	94.155	156	1202.49	**<0.001**
Species	4	22.910	**<0.001**	4	265.594	152	936.89	**<0.001**
SVL	1	47.748	**<0.001**	1	66.606	151	870.29	**<0.001**
Sex × species	4	4.129	**0.003**	4	63.008	147	807.28	**0.006**
Sex × SVL	1	11.519	**0.001**	1	6.95	146	800.33	0.206
Species × SVL	4	2.374	0.055	4	24.346	142	775.98	0.232

	OVS: UV opponency			OVS: saturation			Shoulder: UV opponency			Shoulder: saturation		
							LM					
	df	F	P	df	F	P	df	F	P	df	F	P
Residuals	37			39			21			26		
Sex	1	16.082	**<0.001**	1	26.890	**<0.001**	1	17.239	**<0.001**	1	5.729	**0.024**
Species	2	9.677	**<0.001**	2	26.710	**<0.001**	2	3.931	**0.035**	2	6.649	**0.005**
SVL	1	9.284	**0.004**	1	10.706	**0.002**	1	0.205	0.656	1	6.702	**0.016**
Sex × species	2	4.911	**0.013**	2	5.544	**0.008**	2	2.298	0.125	—	—	—
Sex × SVL	—	—	—	—	—	—	1	0.068	0.797	—	—	—
Species × SVL	2	6.869	**0.003**	—	—	—	2	3.987	**0.034**	2	9.516	**0.001**

Significant values are marked in boldface., SVL, snout–vent length; df, degrees of freedom.

Table 3. Outputs of GLS/GEEGLM models comparing the sex categories

		OVS: UV–blue area		OVS: spot count		OVS: UV opponency		OVS: saturation		Shoulder: UV opponency		Shoulder: saturation	
		GLS model		GEEGLM		GLS model							
All species	df	F	P	Chi^2	P	F	P	F	P	F	P	F	P
(Intercept)	1	28.564	**<0.001**			132.719	**<0.001**	2819.614	**<0.001**	15.288	**<0.001**	4205.164	**<0.001**
Sex category	2	2.393	0.093	4.326	0.115	12.457	**<0.001**	11.396	**<0.001**	2.609	0.081	1.153	0.322
SVL	1	165.226	**<0.001**	12.534	**<0.001**	49.466	**<0.001**	67.611	**<0.001**	0.981	0.326	7.057	**0.010**
SVL × sex category	2	7.845	**0.001**	0.645	0.724	0.588	0.558	0.410	0.665	0.207	0.814	0.575	0.565

species as pseudoreplications (see, e.g., Pekár and Brabec 2016). We ran a marginal model with "sex category," SVL, and their interaction as predictors, affiliation to species and sex as a grouping variable, and we chose a "compound symmetry" correlation structure. Correction for the heterogeneity of variance was also applied. For analysis of the spot count ($n = 288$), we used a generalized estimated equation model (GEEGLM), again with "sex category," SVL, and their interaction as predictors. Poisson distribution was assumed, affiliation to species and sex was set as the grouping variable and ANOVA chi-square test executed. For traits where the sex category was a significant factor, we checked differences between the parthenogens and their ancestral species with planned Tukey's Unequal *N* HSD post hoc test.

We examined the correlation between SVL and UV–blue area for each species and sex with linear regression. The same SVLs may have different interpretations in males and females (Kratochvíl et al. 2003), therefore, we used relative SVL instead for the purpose of plotting, as it better expressed the "ontogenetic time." It is calculated as a proportion of maximum SVL for each species and sex. Data for SVL_{max} were obtained from the literature (Darevsky 1967;

Arakelyan et al. 2011) or from our measurements when our record was higher.

Results

Our results confirmed that UV–blue coloration is sexually dimorphic in *Darevskia* lizards. Proportion of UV–blue area was about 1.4–3.5 times larger in males than in females, depending on the species (Figure 3, Appendix 2). Males also tended to have higher number of spots, higher UV opponency, and higher saturation on both OVS and shoulder (Figure 4, Appendix 2). LMs (GLM in the case of spot count) revealed that sex was a significant factor for all traits ($P \leq 0.024$) along with species ($P \leq 0.005$) and SVL ($P \leq 0.016$) (Table 2). Sex × species interaction was significant for OVS UV–blue area ($P = 0.003$), UV opponency ($P = 0.013$), and saturation ($P = 0.008$). Species × SVL interaction was significant for OVS UV opponency ($P = 0.003$), shoulder UV opponency ($P = 0.034$), and shoulder saturation ($P = 0.001$). Sex × SVL interaction was significant for UV–blue area ($P = 0.001$) (Table 2). Values of the

Table 4. Coefficients of the GLS/GEEGLM models comparing the sex categories

	OVS: UV–blue area Rho = 0.586				OVS: spot count[a]			
	Value	SE	t	P	Estimate	SE	Wald	P
(Intercept)	−13.221	4.696	−2.816	**0.005**	0.960	0.405	5.613	**0.018**
Sex category M	−19.161	6.187	−3.097	**0.002**	1.047	0.675	2.410	0.121
Sex category P	−3.566	5.023	−0.710	0.478	−0.364	1.068	0.116	0.733
SVL	3.465	1.152	3.008	**0.003**	0.031	0.006	26.973	**<0.001**
Sex cat. M × SVL	4.949	1.519	3.259	**0.001**	−0.012	0.011	1.212	0.271
Sex cat. P × SVL	0.891	1.232	0.724	0.470	0.006	0.016	0.161	0.689

	OVS: UV opponency Rho = −0.006				OVS: saturation Rho = 0.120				Shoulder: UV opponency Rho = 0.383				Shoulder: saturation Rho = 0.244			
	Value	SE	t	P	Value	SE	t	P	Value	SE	t	P	Value	SE	t	P
(Intercept)	−123.435	69.403	−1.779	0.079	−9.721	3.679	−2.642	**0.010**	−38.057	128.755	−0.296	0.769	−0.902	2.216	−0.407	0.685
Sex category M	8.821	76.778	0.115	0.909	4.005	4.143	0.967	0.337	6.667	134.058	0.050	0.961	−0.847	3.049	−0.278	0.782
Sex category P	38.287	71.105	0.538	0.592	2.586	3.969	0.652	0.517	30.011	131.597	0.228	0.820	1.503	2.586	0.581	0.563
SVL	31.813	17.419	1.826	0.071	2.996	0.920	3.257	**0.002**	9.879	31.989	0.309	0.758	0.825	0.551	1.497	0.139
Sex cat. M × SVL	−1.031	19.230	−0.054	0.957	−0.934	1.034	−0.904	0.369	−0.064	33.286	−0.002	0.999	0.234	0.755	0.310	0.758
Sex cat. P × SVL	−9.847	17.833	−0.552	0.582	−0.710	0.991	−0.717	0.476	−7.190	32.682	−0.220	0.827	−0.389	0.641	−0.606	0.546

[a] GEEGLM model.,

M, males; P, parthenogens; SVL, snout–vent length.
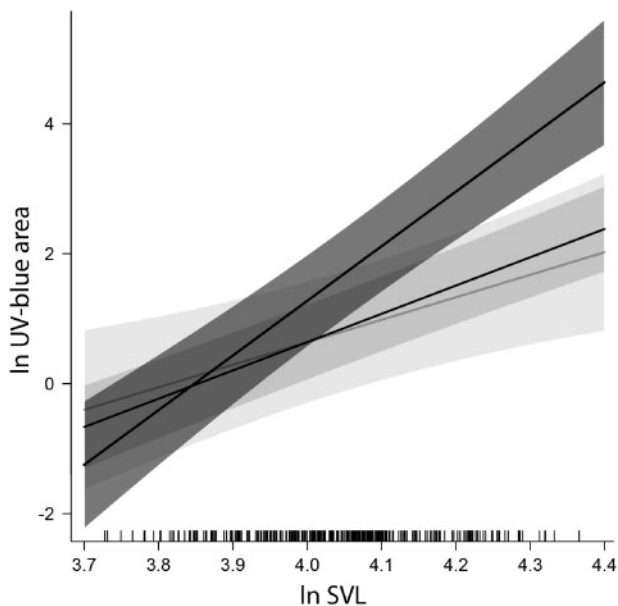
Figure 5. GLS model prediction of the effects of sex categories on the UV–blue area. Dark gray = males, light gray = sexual females, mid gray = parthenogens. Bands show the 95% confidence interval.

parthenogens fell within the range of female values of the related bisexual species.

GLS comparisons of males, sexual females, and parthenogens revealed a significant effect of SVL in UV–blue area ($F_{1,282} = 165.226$, $P < 0.001$), OVS UV opponency ($F_{1,85} = 49.466$, $P < 0.001$), OVS saturation ($F_{1,85} = 67.611$, $P < 0.001$), and shoulder spot saturation ($F_{1,64} = 7.057$, $P = 0.01$). SVL was also significant in the spot count according to GEEGLM ($\chi^2 = 12.534$,

$P < 0.001$). Sex category was significant only in OVS UV opponency ($F_{2,85} = 12.457$, $P < 0.001$) and OVS saturation ($F_{2,85} = 11.396$, $P < 0.001$). SVL × sex category interaction was significant in UV–blue area ($F_{2,282} = 7.845$, $P < 0.001$), which was caused by the effect of males ($t = 3.259$, $P = 0.001$; Table 4). No significant effect of parthenogens was detected in any of the traits, either in sex category alone or in the interaction with SVL (Tables 3 and 4). Effects of each sex category on UV–blue area, as predicted by the GLS model, are plotted in Figure 5.

Examining each species separately, we found positive correlation between SVL and OVS UV–blue area mainly in the males (*D. r. raddei*: $r = 0.498$, $P = 0.025$; *D. r. nairensis*: $r = 0.791$, $P < 0.001$, *D. caucasica*: $r = 0.552$, $P = 0.041$, *D. mixta*: $r = 0.625$, $P = 0.016$), but also in females *D. r. raddei* ($r = 0.819$, $P = 0.004$) and in all parthenogens except *D. rostombekowi* (*D. armeniaca*: $r = 0.442$, *D. dahli*: $r = 0.606$, *D. unisexualis*: $r = 0.767$; all $P \le 0.001$; Figure 6).

Planned post hoc tests found no significant difference in the UV–blue area between the parthenogenetic species and females of their respective ancestral bisexual species. The only exception was *D. dahli*, which had significantly smaller UV–blue area compared with females of its paternal ancestor *D. portschinskii* ($P = 0.011$). When taking into account the data for the ethanol-fixed *D. mixta*, a significant difference between *D. armeniaca* and females of *D. mixta* also appeared, with *D. armeniaca* having larger UV–blue area ($P = 0.001$).

Discussion

We have confirmed sexual dimorphism in both quantitative and chromatic parameters of the UV–blue traits in *Darevskia* lizards. Our results are consistent with other studies on lacertids showing that the blue/UV–blue lateral spots occupy larger area and/or are more numerous in males than in females, for example,
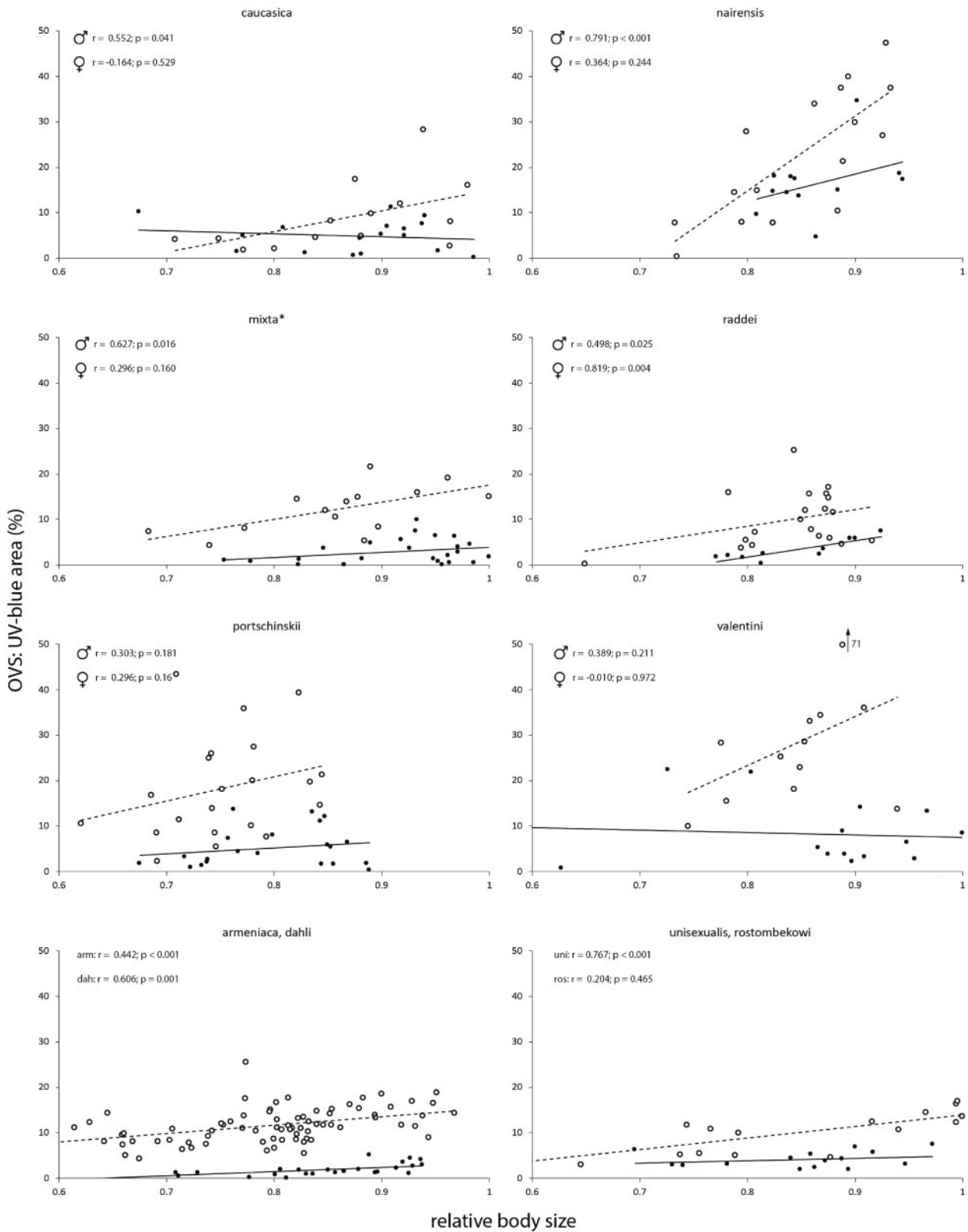
Figure 6. Correlation between relative body size (proportion of maximum SVL recorded for each species and sex) and OVS UV–blue area in bisexual and parthenogenetic lizards. Open dots + dashed lines: males, *D. armeniaca, D. unisexualis*; full dots + solid lines: sexual females, *D. dahli, D. rostombekowi*. *Values of *D. mixta* are based on measurements of ethanol-fixed individuals.

Psammodromus algirus (Carretero 2002), *G. galloti* (Molina-Borja et al. 2006), *T. lepidus* (Font et al. 2009), *P. muralis* (Names et al. 2019). Significant sex × species interactions in the LMs confirm that sexual dimorphism in OVS (UV–blue area, spot count, and chromatic parameters) varies considerably across the species (Figure 6). The same was not proven for the shoulder spots, however, this could have been caused by small sample sizes in this particular subset of data. Despite the high interspecific variability, the GLS model predicts a general tendency of OVS UV–blue area to grow with body size in males, rather than females (Figure 5), which is also consistent with observations in *Podarcis* lizards (Names et al. 2019).

The GLS model/GEEGLM did not reveal any systematic difference between the parthenogens and sexual females. The most noticeable distinction between these 2 groups appears when considering each parthenogenetic species separately. Three out of 4 species (*D. armeniaca, D. unisexualis,* and *D. dahli*) show a positive correlation between SVL and UV–blue spot area, which is a feature typical of males, but not sexual females. In general, the slope of the parthenogens corresponds to the slope of sexual females according to the GLS model prediction (Figure 5), but correlation coefficients are higher in the parthenogens (Figure 6). Therefore, we cannot rule out that the correlation can be present in sexual females as well, but was not detected due to their higher variance and lower sample sizes.

Our results did not confirm the hypothesis that UV–blue ornamentation in the parthenogenetic females would become either less or more conspicuous than in sexual females due to the absence of males. Based on our data, the only candidate for a notably duller parthenogen is *D. dahli*. It has significantly smaller UV–blue area than females of its paternal ancestor *D. portschinskii*, but whether the same applies to the difference from its maternal ancestor *D. mixta* is a matter of question. Our test did not detect a significant difference. Nonetheless, our samples of *D. mixta* were ethanol-fixed specimens, so the areas of their UV–blue spots could have been underestimated and a false negative result obtained. *Darevskia dahli*, however, is just 1 of 7 known parthenogenetic species of the genus *Darevskia*, each of them having a fairly distinct phenotype. We find larger and "UV-bluer" (e.g., *D. armeniaca, D. unisexualis*) as well as smaller and duller parthenogenetic species (e.g., *D. dahli, D. rostombekowi*) within the genus, which applies to both quantitative and chromatic qualities of the UV–blue ornaments (Figures 3 and 4). The reason why the parthenogens showed no systematic tendency toward lower (or higher) conspicuousness may be just a consequence of this diversity, which apparently arose from their hybrid origin. Each parthenogenetic species has a unique combination of parental genomes (Moritz et al. 1992; Freitas et al. 2019), which leads to different expression of UV–blue ornaments in each of the hybrids. These phenotypes could have been established at the genesis of the clones and then conserved by clonal reproduction (Abramjan et al. 2019).

The result that the parthenogens do not significantly differ from sexual females is much harder to interpret in terms of various selective pressures, as their effect is not so obvious in such a case. Considering predation, for instance, it can be stated that it does not reduce the UV ornaments in the parthenogens, because they are not very costly. This can be either due to signal partitioning (the spots restricted to OVS are exposed to the conspecifics, but hidden from the sight of aerial predators; Marshall and Stevens 2014), or the ornaments had been already selected for a "safe amount of conspicuousness" and do not need any further reduction. Shoulder spots, however, may respond differently. Unlike OVS, they cannot be concealed from predators. Our results suggest their chromatic qualities are comparable between sexual and parthenogenetic

females, but we did not examine their sizes and counts. Hence, we cannot rule out that these may vary between the 2 groups. Furthermore, some species like *D. valentini* or *D. mixta* were not available to us for chromatic measurements and their inclusion in further studies would help to draw a more accurate image.

Our study was aimed mainly on the UV–blue coloration itself. Besides, chromatic properties only were assessed in the shoulder spots. A complex coverage of various species and evaluation of their overall pattern would be desirable in further research, especially focusing on the coloration of the back, belly, and the lateral flanks, and taking into account the natural background and variation between populations of the same species.

Acknowledgments

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Appendix 1: List of Material Used in This Study

Species	Population	Country	Males	Females
Bisexual				
Darevskia caucasica	Kazbek	Georgia	9	12
Darevskia caucasica	Tusheti	Georgia	5	5
Darevskia mixta[a]	Bakuriani	Georgia	7	18
Darevskia mixta[a]	SW of Tbilisi	Georgia	7	6
Darevskia raddei nairensis	Hayrivank	Armenia	9	8
Darevskia raddei nairensis	Yerevan	Armenia	7	4
Darevskia raddei raddei	Geghard	Armenia	8	3
Darevskia raddei raddei	Tatev	Armenia	12	6
Darevskia raddei raddei	Gosh	Armenia		1
Darevskia portschinskii	Kojori	Georgia	12	15
Darevskia portschinskii	Gori	Georgia	5	5
Darevskia portschinskii	Gosh	Armenia	4	1
Darevskia valentini	Lchashen	Armenia	8	7
Darevskia valentini	Kuchak	Armenia	1	1
Darevskia valentini	Sepasar	Armenia	3	7
Parthenogenetic				
Darevskia armeniaca	Dilijan	Armenia		60
Darevskia armeniaca	Lchashen	Armenia		3
Darevskia armeniaca	Hankavan	Armenia		13
Darevskia dahli	Kojori	Georgia		12
Darevskia dahli	Dilijan	Armenia		13
Darevskia rostombekowi	Dilijan	Armenia		15
Darevskia unisexualis	Sevan	Armenia		15

[a] Material from the collections of the Zoological Museum in Moscow.

Appendix 2: Mean, Minimum, and Maximum Values for Quantitative and Chromatic Parameters of UV–Blue Spots

Quantitative parameters			SVL (mm)			OVS: UV–blue area (%) per row			OVS: UV–blue spots count per row		
species	Sex	N	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Bisexual											
Darevskia caucasica	F	17	55.92	43.2	63.1	5.0	0.2	11.3	7.0	0	17
Darevskia caucasica	M	14	52.84	43.2	59.8	8.9	1.8	28.3	8.8	0	19
Darevskia mixta[a]	F	24	55.59	45.7	60.7	2.9	0.0	10.0	4.0	0	9
Darevskia mixta[a]	M	14	54.14	43.0	63.0	12.2	4.3	21.6	8.3	6	13
Darevskia raddei nairensis	F	12	59.59	55.8	65.2	16.4	4.7	34.6	11.4	2	15
Darevskia raddei nairensis	M	16	61.98	53.5	68.1	22.9	0.4	47.2	11.9	1	21
Darevskia raddei raddei	F	10	56.51	51.7	61.9	3.3	0.3	7.4	3.6	0	18
Darevskia raddei raddei	M	20	58.04	44.8	63.2	10.1	0.2	25.3	7.3	3	15
Darevskia portschinskii	F	21	51.89	43.9	57.8	5.2	0.4	13.7	7.2	0	20
Darevskia portschinskii	M	21	50.49	41.6	56.6	18.4	2.2	43.4	14.9	7	20
Darevskia valentini	F	15	67.45	46.8	78.7	8.3	0.8	22.4	11.6	3	21
Darevskia valentini	M	12	67.57	59.6	75.2	28.1	10.0	71.3	16.6	12	23
Parthenogenetic											
Darevskia armeniaca	F	76	58.39	44.9	70.6	11.7	4.4	25.6	9.8	3	15
Darevskia unisexualis	F	15	62.82	47.1	73.0	9.9	3.0	17.0	9.4	0	13
Darevskia dahli	F	24	54.54	45.4	60.0	1.8	0.0	5.2	3.9	0	9
Darevskia rostombekowi	F	15	51.00	41.7	58.3	4.1	1.9	7.4	5.1	0	10

Chromatic parameters			OVS: UV opponency			OVS: saturation				Shoulder: UV opponency			Shoulder: saturation		
Species	Sex	N	Mean	Min	Max	Mean	Min	Max	N	Mean	Min	Max	Mean	Min	Max
Bisexual															
Darevskia raddei nairensis	F	4	12.70	6.49	17.10	17.40	11.60	22.78	4	6.21	5.49	7.81	12.10	11.68	13.24
Darevskia raddei nairensis	M	10	12.34	−5.32	19.14	16.81	9.02	22.60	10	9.16	3.14	14.40	13.04	9.45	17.82
Darevskia raddei raddei	F	3	−2.27	−10.81	7.22	10.33	9.24	11.43	3	−0.97	−7.56	5.83	9.35	8.37	9.87
Darevskia raddei raddei	M	8	9.38	−5.47	19.65	13.98	6.56	22.32	7	4.59	−2.46	8.40	11.08	9.23	13.92
Darevskia portschinskii	F	11	1.45	−3.35	8.04	6.45	4.64	10.99	4	−0.35	−12.00	9.54	12.59	11.15	14.56
Darevskia portschinskii	M	10	6.41	3.92	9.79	10.08	6.81	13.74	5	11.06	2.79	15.69	13.86	6.65	19.20
Darevskia valentini[b]	M	1	8.83	—	—	11.69	—	—	—	—	—	—	—	—	—
Parthenogenetic															
Darevskia armeniaca	F	14	5.68	−1.37	9.93	9.80	5.28	14.22	14	6.57	−0.67	11.71	11.35	6.13	15.79
Darevskia unisexualis	F	7	5.37	1.62	9.90	11.43	6.84	17.01	8	6.16	3.92	9.46	12.64	9.21	16.53
Darevskia dahli	F	14	2.02	−6.03	6.44	6.69	4.05	9.22	11	−2.00	−7.86	4.49	9.15	7.42	12.30
Darevskia rostombekowi	F	10	2.12	−2.40	7.27	6.83	4.99	10.35	4	0.30	−7.43	4.36	9.85	8.62	10.75

[a] Values of *D. mixta* are based on measurements of ethanol-fixed individuals., [b] An individual of *D. valentini* not included in the analyses of chromatic parameters.