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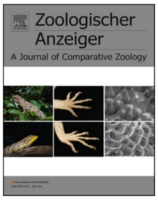

Reproductive effort of unisexual and bisexual rock lizards (genus *Darevskia*)

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ABSTRACT

We compared the life history components of small and large-bodied unisexual (*Darevskia dahli* and *Darevskia armeniaca*) and bisexual (*Darevskia portschinskii*, *Darevskia valentini,* and *Darevskia obscura*) Caucasian rock lizard species. Research objectives were to determine whether reproductive mode (bisexual or parthenogenetic), female body size, altitude and landscape of the habitat, or interaction of these factors determine the relative investment of energy into a single reproduction, number, and relative size of eggs.

The research revealed the differences between two parthenogenetic species and their paternal bisexual lizards. However, the pattern did not coincide for the two studied lineages i.e., parthenogenetic *D. armeniaca* invests relatively more resources into reproduction than its paternal *D. valentini*. Simultaneously, reproductive effort of parthenogenetic *D. dahli* did not differ from its paternal *D. portschinskii*. Instead, *D. dahli* tended to produce more but lighter eggs than *D. portschinskii*. In both cases, the parthenogenetic form tended to follow a *r*-reproductive strategy, typical for lizards occupying less stable environments than their parental species. However, other interspecific differences such as body size or evolutionary distance shade these differences, and determine the pattern of divergence between a parthenogen and its bisexual relative. In particular, smaller body size constrains increased the reproductive effort, and parthenogenetic species shifted to a balance between egg size and number rather than between resources invested into a single reproduction event and the probability to survive until the next season.

1. Introduction

Organisms with multiple reproductive cycles distribute their energy resources throughout their lifetime, considering growth, survivorship, and reproductive success (Stearns 1977; 1992; Congdon, 1989; Macip-Ríos et al., 2017). According to the life-history theory, explaining how natural selection leads organisms to optimize their survival rates and reproduction (Stearns, 1992; Roff, 1992; Stearns et al., 2000; Fabian and Flatt, 2012), these variables are key factors for increasing the fitness of an animal (Babich Morrow et al., 2021). Because the resources are limited, organisms cannot simultaneously increase individual survival rates and reproductive investment, and the observed balance results from the tradeoffs between those (Babich Morrow et al., 2021). Charnov and his co-authors (Charnov and Downhower 1995; Charnov and Berrigan 1991; Charnov 1993; 2002; Babich Morrow et al., 2021) developed three-dimensional metrics to quantify fundamental life-history tradeoffs: lifetime reproductive effort (LRE), relative reproductive lifespan (RRL), and relative offspring size (ROS). LRE measures the proportion of adult mass that a female will allocate to offspring over her lifespan (Charnov, 2002; Babich Morrow et al., 2021); RRL quantifies time to maturity relative to the total amount of time available for reproduction (Charnov, 1993; Charnov, 2002; Babich Morrow et al., 2021); and ROS is the ratio of offspring size to adult size (Millar 1977; Babich Morrow et al., 2021). The other tradeoff in Life-history, one between the number and size of offspring, confirmed to vary at both interspecific and intraspecific levels, coinciding with *r*- and *K*- evolutionary strategies (Stearns, 1989; Tarkhnishvili, 1993; Roff, 2002; Brown and Shine, 2009).

In oviparous vertebrates with multiple reproductive cycles and without expressed parental care, such as most lizards, the tradeoff between life history parameters can be presented in a simple diagram (Fig. 1). An increase of energy share, invested into a single reproduction, increases the potential number of viable offspring during one season but decreases the probability of a female surviving until the next season (Qualls and Shine, 1998). Given the same female body mass and reproductive effort, an increase in the number of eggs is associated with

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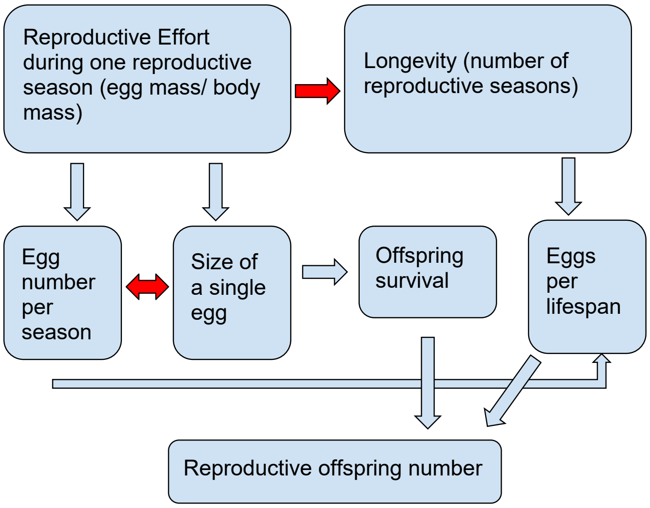

Fig. 1. Interdependence among the components of life history. Reproductive effort increases te number and/or survival of offspring per season but decreases the potential number of reproductive seasons. Increase of an egg size positively affects offspring survival, but negatively - the number of eggs per reproductive season. Egg number and offspring survival both positively affect fitness. Red arrows show negative effects. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

a decrease in egg size. Egg size potentially increases the probability of a single egg to survive until hatching and that of a juvenile to survive in the first months of its life (Sinervo, 1990; Levitan, 2006).

Lizards are classical objects for studying tradeoffs between the components of reproductive strategies. Their reproductive characteristics vary both between conspecific populations and between closely related species. For example, Boretto et al. (2018) described variation of reproductive effort of iguanids from the genus *Phymaturus* depending on the altitude. Inter-population variations in egg size, clutch size, and reproduction frequency is shown for another iguanid, *Sceloporus undulatus* (Tinkle and Ballinger, 1972). In ornate tree lizards (*Urosaurus ornatus*), clutch size depends on the habitats (trees vs rocks) they occupy (Haenel, 2011). In general, reproductive period, clutch size, and egg size of lizards strongly depend on the environmental variables (Shine and Elphick 2001; Brandt and Navas, 2011; Menezes and Rocha, 2014), including temperature (Cruz, 1996; Ramírez-Bautista et al., 2000; Rezende-Pinto et al., 2009; Menezes and Rocha, 2014), rainfall (Rodríguez-Ramírez and Lewis 1991; Ramírez-Bautista et al., 2000; Martelotte et al., 2010, Menezes and Rocha, 2014), habitat type (Haenel, 2011) and food availability (Fitch, 1982; Haenel, 2011). In addition, reproductive variables in lizard populations depend on the female body size (Vrcibradic and Rocha 2011; Winck and Rocha 2012; Menezes and Rocha, 2014). Females with larger bodies may produce larger and heavier eggs (Brandt and Navas, 2011; Menezes and Rocha, 2014), although the effect of body size depends on a specific taxonomic group (Stewart, 1979; Sinervo, 1990; Schwarzkopf, 1992; Doughty 1997). Ljungström et al. (2016) found that the additive genetic component determining the variation of egg size and number within species is minute; hence, the tradeoff between reproductive variables may change during a lifespan of a single animal.

Last but not least, some groups of lizards have both sexual breeding and parthenogenetic taxa, which may also affect the reproductive strategy. Schall (1978) presented the data on five species sympatric in southwest Texas, two of which are parthenogenetically reproducing. The bisexual and unisexual species did not differ in clutch size, egg size, or clutch/body weight ratio, and some interspecific differences in reproductive characteristics were attributable to different body sizes. On the other hand, Congdon et al. (1978), based on the study of two bisexual and two parthenogenetic *Aspidoscelis* from Arizona, concluded that the unisexual species have larger clutches, increase clutch size faster with body size, have lighter eggs, and higher clutch/body calorie ratios than the closely related bisexual species - irrespective of body size of a species.

In this paper, we compared the components of life history in the two parthenogenetic and three bisexual species of Caucasian rock lizards (*Darevskia* Arribas, 1999) from three locations in Georgia. The parthenogenetic forms ("species") in these locations coexist either with their paternal sexual breeders, or with a closely related bisexual species, but not ancestral to them. The parthenogens and their ancestors differ in body size and preferred altitudes. Our purpose was to explore if and how the mode of reproduction (sexual vs parthenogenetic) affect reproductive characteristics of a female (including reproductive effort, egg size, egg number, or the trade-off among these parameters), and whether this effect depends on the other variables, such as body size of a female, altitude of a habitat, or phylogeny.

2. Materials and methods

2.1. Research organisms

Genus *Darevskia* is a speciose group of small-bodied lizards. Their average lifespan is five to six years (Arakelyan & Danielyan, 2000; Galoyan et al., 2019) and they usually reproduce during several seasons. *Darevskia* differ from each other in the reproductive mode (bisexual vs unisexual), body size (SVL varying between 58 cm) (Darevsky et al., 1985; Galoyan et al., 2019) and preferred altitudinal range (Darevsky et al., 1985; Tarkhnishvili, 2012). Our study organisms were two hybrid parthenogenetic species of the genus from Georgia, *Darevskia dahli* (Darevsky, 1957) and *Darevskia armeniaca* (Méhely, 1909) and their paternal species, *Darevskia portschinskii* (Kessler, 1878) and *Darevskia valentini* (Boettger, 1892), respectively, which commonly share habitats with the daughter parthenogens (Murphy et al., 2000; Tarkhnishvili et al., 2020). Fifth species we studied was *Darevskia obscura* (Lantz and Cyrén, 1936), phylogenetically equidistant from *D. portschinskii* and *D. valentini*.

The first pair of the parthenogen and its ancestor, *D. dahli* and *D. portschinskii*, coexist in the mountain forest belt of central Georgia, 800–1200 m a.s.l (Tarkhnishvili et al., 2010). Adult body length of both species varies between 5.4 and 5.8 cm. The second pair of species, *D. armeniaca* and *D. valentini*, coexist at the elevations 1900–3100 m (Arakelyan et al., 2011; Galoyan et al., 2019). Body of these species is larger than the species of the previous pair, with body length varying between 6.1 and 6.4 cm. There are some locations where *D. armeniaca* coexist with a non-ancestral, *D. obscura,* sympatric with *D. armeniaca* within the elevation range 1500–1800 m a.s.l (Darevsky et al., 1985; Tarkhnishvili, 2012).

2.2. Sampling

In May–June, 2019-2021-2022, females of five species of rock lizards were collected from three locations in Georgia, total sample size - 87 (13–26 individuals per species) (Table 1)). Sample sizes for individual species were modest, however, we considered that catching more lizards could potentially affect the respective populations dynamics if egg incubation was unsuccessful, and further increasing sample size could cover several more years of work. The females in which mature follicles were palpated (all bisexual individuals had mating marks) were placed into plastic containers with moss and soil, daily fed with crickets, and released after the eggs were deposited. Eggs were further kept on slightly humid soil under room temperature (ca. 25–30 °C) until juveniles were hatched (Fig. 2). Every female was measured with calipers and was weighed after capturing and after egg deposition on electronic scales with precision 0.1 g. Each egg was weighted with the same scales not later than in 7–8 h after the deposition, and egg maximum diameter was measured with calipers to precision 0.1 mm. During measuring eggs

Table 1
Sample sizes (gravid female lizards) and key characteristics of the sampling location of six species of *Darevskia*.

Species	Location	Easting	Northing	Alt. a.s.l.	Sample size	Rep. mode
D. dahli	Kojori	44.68°	41.64°	1120	17	unisexual
D. portschinskii	Kojori	44.68°	41.64°	1120	16	bisexual
D. armeniaca	Sagamo Lake	43.73°	41.29°	2015	11	unisexual
D. armeniaca	Riv.Kirkhbulakhi	43.73°	41.29°	1715	15	unisexual
D. valentini	Sagamo Lake	43.73°	41.29°	2015	15	bisexual
D. obscura	Riv.Kirkhbulakhi	43.73°	41.29°	1715	13	bisexual

Fig. 2. Stages of egg deposition and hatching of individuals of *D. armeniaca* individual at laboratory.

artificial damage was maximally avoided. The weighting procedure was repeated after hatching of the juveniles. Females and juveniles were released after several weeks.

2.3. *Statistical analysis*

From the original measurements, we calculated several derivative variables, hence increasing the number of the reproductive characteristics of each individual. The characteristics of each individual and egg is given in supplementary Table A.1. The reproductive variables used in the further analysis were: (1) female body mass before (FMB) and (2) after (FMA) egg deposition; (3) female body length from the tip of the snout to the hind angle of hip and body junction (FL); (4) Egg number (EN); (5) Average egg mass in a clutch (AEM); (6) clutch mass (total mass of the eggs; CLM); (7) reproductive effort (RE) calculated as the proportion of clutch mass to female body mass before the egg deposition; (8) Relative egg mass (REM) - proportion of average egg mass to FMB; (9) Egg shape (ESH) - maximum diameter of egg divided on the egg mass.

We assume that the altitude of the location, mode of reproduction (sexual vs parthenogenetic), FMB, FMA, and FL are predictors, whereas all other reproductive variables are dependent on these predictors and on each other.

We tested the significance of the differences between the studied populations, correlation/association between the variables using a combination of simple statistical methods: (1) we used one-way ANOVA to infer significant differences between the populations in the studied reproductive variables. We used post-hoc analysis using Bonferroni method to identify those populations which show significant differences in average values. (2) General Linear Model (GLM) was applied to infer the influence of the predictors on each dependent reproductive variable separately, across the species and populations. (3) we calculated Pearson correlation matrix in order to find the dependencies between the reproductive variables separately for each studied species. All calculations were done in IBM SPSS software (2021).

3. Results

3.1. *Interspecific comparisons*

Most variables related to reproduction showed significant differences among the study species, with the exception of absolute and relative egg mass, which showed near-significant differences (one-way ANOVA; Table 2). As expected, *D. armeniaca* and *D. Valentini* (both species living at higher altitudes) had longer and heavier bodies, heavier clutches, and more eggs in clutch than *D. portschinskii* and *D. dahli* living at lower altitudes; the differences being mostly significant (see Table 2). Female *D. obscura* were larger, had more eggs and heavier clutches than *D. portschinskii* and *D. dahli*, hence the differences were species-specific and were not related solely to altitude. Simultaneously, *D. obscura* and *D. armeniaca* (but not *D. valentini*) had significantly heavier eggs than the

Table 2
Interspecific differences of reproductive biology traits among six lizard species (genus *Darevskia*) using a One-way ANOVA.

Variable	df within/ between groups	F	P	Post-Hoc (Bonferroni), P < 0.05
FL	5/81	14.044	<0.001	a1>d; a2>d; o>d; v>d; a1>p; a2>p; o>p; v>p
FMB	5/81	22.687	<0.001	a1>d; a2>d; o>d; v>d; a1>p; a2>p; o>p; v>p
FMA	5/81	16.967	<0.001	a1>d; a2>d; o>d; v>d; a1>p; a2>p; o>p; v>p
EN	5/81	13.510	<0.001	a1>d; a2>d; v>d; v>p; o>p
AEM	5/81	5.626	<0.001	a2>d; a2>p; o>d; o>p
AEL	5/81	1.887	0.106	–
CLM	5/81	20.014	<0.001	a1>d; a2>d; o>d; v>d; a1>p; a2>p; o>p; v>p
RE	5/81	5.777	<0.001	a2>d; o>d; a1>p; a2>p; o>p
REM	5/81	4.583	0.001	v>a2; v>p
ESH	5/81	7.096	<0.001	a1>p; a2>p; o>p; o>d

FL - body length of a female, FMB and FMA - female weight before and after the egg deposition, RE - reproductive effort, REM - relative egg mass (proportion of average egg mass to FMB). a1 – *Darevskia armeniaca* (Riv. Kirkhbulakhi), a2 - *D. armeniaca* (Saghamo Lake), d - *D. dahli*, o - *D. obscura*, p - *D. porschinskii*, v - *D. valentini*.

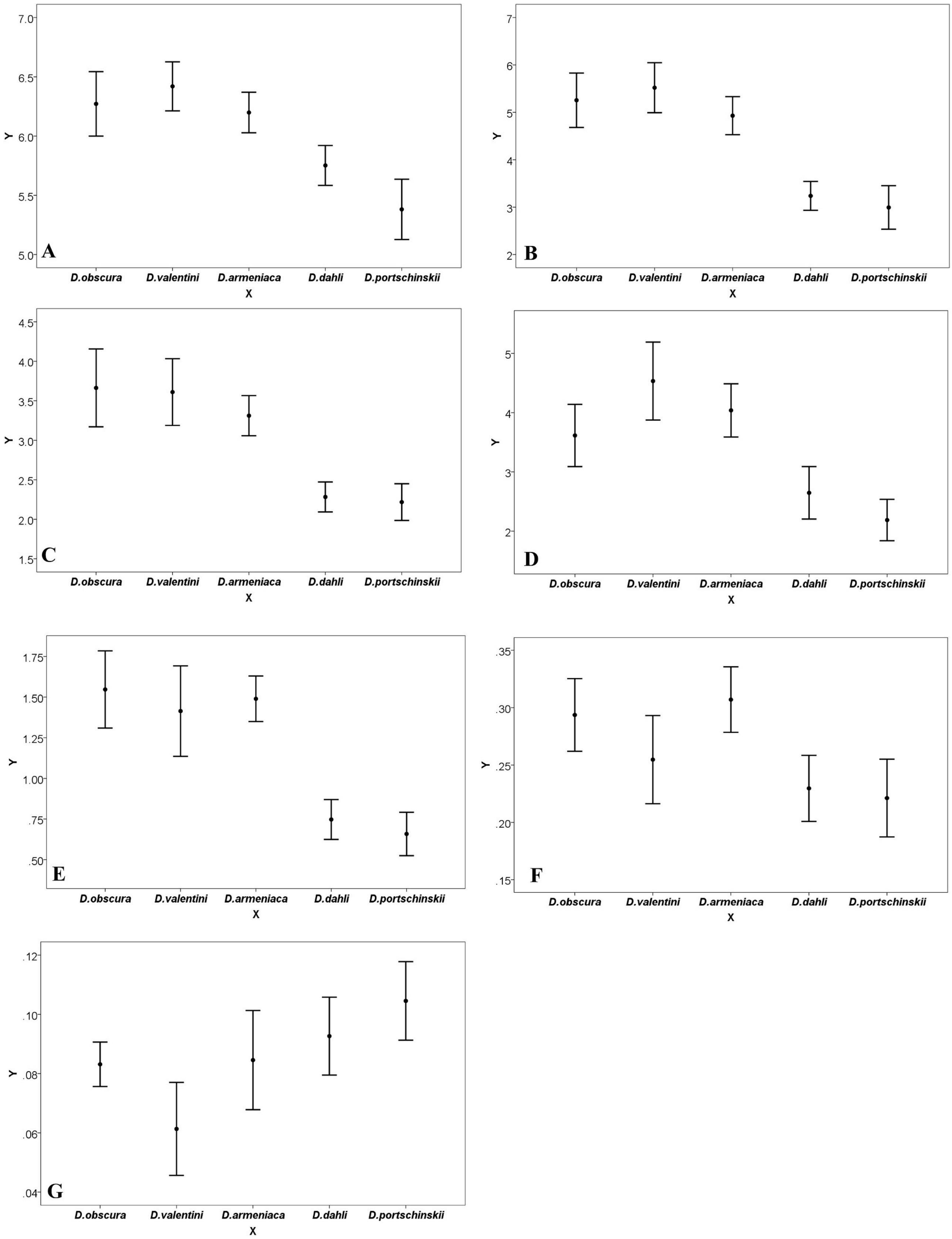

Fig. 3. A–G. Gravid female individuals of five species on X - axis with body lengths (A), body weight before (FMB) (B), body weight after (FMA) (C), number of eggs (EN) (D), clutch weight (CLM) between small and large – bodies species (E), Reproductive effort (RE) (F), Relative egg weight (REM) (G) on Y - axis with 95% confidence Interval.

Table 3
Impact of reproductive mode, altitude, and female body mass on reproductive biology traits. A general Linear Model was applied using reproductive mode and altitude as fixed factors, and female mass as covariate. P values are shown; P values ≤ 0.05 highlighted in bold.

	CLM	RE	AEM	EN	REM	ESH
FMB	0.338	0.040	0.004	<0.001	<0.001	0.149
FMA	0.065	0.185	0.015	0.343	0.010	0.212
FL	0.192	0.117	0.051	0.633	0.107	0.226
Altutude	0.008	0.002	0.009	0.458	0.039	0.004
rep.mode	0.163	0.115	0.927	0.089	0.883	0.412
Alt_repr. mode	0.126	0.095	0.003	0.090	0.010	0.045

FMB and FMA - female weight before and after the egg deposition, FL - body length of a female, rep.mode-reproductive mode, Alt_repr.mode – Altitude with reproductive mode, CLM – total mass of the eggs, RE - reproductive effort, AEM – average egg mass, EN – egg number, REM - relative egg mass, ESH – egg shape.

other three species (Fig. 3A–D). Reproductive effort of these species was also higher than in *D. portschinskii* and *D. dahli*; *D. valentini* was intermediate in this respect (Fig. 3 E). Conversely, *D. portschinskii* and *D. dahli* had a higher relative egg mass than the other species, although significantly exceeded only *D. valentini*'s relative egg mass (Fig. 3 F). Finally, these two species had more elongated eggs than *D. armeniaca* and *D. obscura*, whose eggs were more round in shape (Fig. 3 G).

3.2. Interspecific life history trade offs

Female body mass across species significantly affected the number of deposited eggs and relative egg mass, but not reproductive effort or absolute egg mass (see Table 3). Larger-bodied species deposited more eggs but each egg was lighter in proportion to female body mass. Clutch mass, average and relative egg mass, and reproductive effort were higher in species living at higher altitudes, although the altitude hardly affected these variables directly: simply, the larger lizard species lived at higher altitudes. Reproductive mode by itself influenced egg mass (*D. armeniaca* had heavier eggs than *D. valentini*), and in interaction with the altitude of the location, it had a significant effect on reproductive effort and both average and relative egg mass. Hence, while reproductive mode had an effect on some reproductive variables, the direction of this effect was not consistent and depended on other characteristics such as altitude or the specific evolutionary lineage of the lizard.

3.3. Intraspecific life history trade offs

Within *D. armeniaca, D. dahli,* and *D. valentini*, increased female body mass positively correlated with clutch size and egg number (although in *D. portschinskii* and *D. obscura*, the correlation was not significant), and negatively with relative egg mass respectively (see Table 4). Average egg mass was positively related to female body mass in *D. obscura* and *D. portschinskii*, but negatively in *D. armeniaca* (the correlation was not significant in *D. dahli* and *D. valentini*). Average egg mass also negatively correlated with egg number in *D. armeniaca*; but the correlation was not significant in the other lizard species investigated (see Table 4). In *D. armeniaca* and *D. valentini* (but not in three other lizad species) the absolute and relative egg mass increased with reproductive effort. In short, there were obvious patterns of interspecific differences that could not be generalized when comparing species with having variable modes of reproduction i.e., *D. valentini* and especially *D. Armeniaca* invested more resources into egg number than in egg size during growth, whereas female *D. portschinskii*, and *D. obscura* invested more into egg size. In *D. armeniaca* this trend was especially strong as heavier females produced more but even lighter eggs. The reproductive effort was not directly associated with female body size, although female *D. armeniaca* and *D. valentini* invested relatively more resources into a single reproduction event by producing heavier eggs, whereas *D. portschinskii*, *D. dahli*, and *D. obscura* produced more eggs.

4. Discussion

Reproductive characteristics of five lizard species, described in this paper, slightly differ from that described in Darevsky (1967) and Galoyan et al. (2019). The number of eggs per clutch and egg diameter was less than reported by these authors (Table 5). These differences may be associated with the different way of sampling: we measured the eggs deposited a few hours before, whereas Darevsky (1967) measured oocytes from ovaria or eggs found in nature. Darevsky (1967) suggested that Caucasian rock lizards, with few exceptions of particularly big females, deposit only one clutch per season, hence the differences are related to the population specifics rather than to the presence of additional clutches.

There are significant differences in the reproductive parameters of the studied species. We cannot attribute these differences solely to the mode of reproduction, body size, or any other predictor. Rather, there is a complex interaction between the variables associated with a particular species that determine reproductive effort, relative size and number of eggs. It is also important to consider how the need to house females in captivity could have affected some of our variables. In particular, FMA (which could be considered a more independent measure of female body size than FMB) was highly variable and dependent on the condition of the females after egg deposition. Some females were kept longer than the others before the egg deposition, and differences in their feeding rate in captivity may have influences FMA. Ideally, we would be able to measure female body mass before they were gravid, but because we were not able to obtain that information, we emphasized FMB in our analyses. However, the correlations between our variables and FMA (Table 4) are in the same direction as correlations with FMB.

Our findings can be summarized as the following: (1) Species with larger females produce heavier clutches, deposit more eggs, and invest relatively more resources into a single reproduction than small-bodied species. Besides, the eggs of small-bodied species are elongated, and the eggs of bigger ones are more round; (2) *D. armeniaca* invests larger portion of its body mass in a single reproduction than its paternal *D. valentini*, it deposits heavier eggs relative to its body size, although clutch size or egg size and number don't differ in two species; (3) larger *D. dahli* deposit more eggs than smaller ones, although not heavier eggs. In contrast, larger individuals of its paternal *D. portschinskii* from the same location deposit heavier eggs than the smaller individuals; (4) *D. obscura* invests more resources in a single reproduction than two other sexual breeders, and it deposits heavier eggs.

Our results suggest complex, species-specific relationships between reproductive variables. On the first glance, it is difficult to recognize a clear pattern in this butch of correlations. However, some of those are easily explained. The concept of *r/K* reproductive strategy, introduced by MacArthur and Wilson (1967) attempts to explain the differences between species dependent on less vs more stable environments. In an unstable environment, a species allocates more resources into the offspring number and hence rapidly reproduces in short periods when the environmental conditions are good (*r* - strategy), whereas in stable environmental conditions allocating more resources in each individual offspring is more favorable (Pianka, 1970). More precisely, optimization of reproductive strategy considers trade-offs between: total parental investment/reproductive effort (RE), offspring number, and offspring quality (Tuomi et al., 1983; Morris, 1987; Stearns, 1992). In animals with no parental care, "offspring quality" should be tightly related to egg size: heavier eggs are less dependent on the environmental fluctuations. High RE may decrease the probability of a female to survive until the next reproductive season (Vitt and Caldwell, 2014), and it may also be associated with a less stable environment.

Parthenogenetic lizards reproduce more rapidly than the sexual breeders; they form larger populations and occupy a larger share of suitable habitats (Tarkhnishvili et al., 2010; Tarkhnishvili, 2012). Barateli et al. (2021) showed that, for *D. dahli* and *D. portschinskii*, these differences are observed even on microhabitat scale. Wright and Lowe

Table 4
The correlations between all variables within species. Pearson correlation. Significance coefficient is shown by * (* = <0.05; ** < 0.01; *** < 0.001)

Species		FL	FMA	FMB	AEL	AEM	EN	CLM	ESH	RE	REM
D.armeniaca	FL	1	.764***	.754***	.015	-.125	.590**	.544**	.041	-.109	-.381
	FMA	.764***	1	.918***	.173	-.214	.666***	.545**	.177	-.272	-.520*
	FMB	.754***	.918***	1	.046	-.393*	.829***	.558**	.283	-.354	-.690**
	AEL	.015	.173	.046	1	.109	-.083	.019	.198	-.042	.081
	AEM	-.125	-.214	-.393*	.109	1	-.612**	.267	-.887***	.726***	.920***
	EN	.590**	.666***	.829***	-.083	-.612**	1	.558**	.433*	-.222	-.777***
	CLM	.544**	.545**	.558**	.019	.267	.558**	1	-.427*	.557**	-.005
	ESH	.041	.177	.283	.198	-.887***	.433*	-.427*	1	-.809***	-.790***
	RE	-.109	-.272	-.354	-.042	.726***	-.222	.557***	-.809***	1	.725***
	REM	-.381	-.520**	-.690***	.081	.920***	-.777***	-.005	-.790***	.725***	1
D.dahli	FL	1	.569*	.800***	-.202	-.099	.459	.435	-.012	.066	-.622**
	FMA	.569*	1	.810***	-.153	.235	.415	.576*	-.366	.185	-.437
	FMB	.800***	.810***	1	-.406	-.143	.646**	.584*	-.034	.111	-.790***
	AEL	-.202	-.153	-.406	1	.670**	-.436	-.025	-.219	.210	.610**
	AEM	-.099	.235	-.143	.670**	1	-.385	.250	-.855***	.342	.696**
	EN	.459	.415	.646**	-.436	-.385	1	.791***	.230	.604*	-.754**
	CLM	.435	.576*	.584*	-.025	.250	.791***	1	-.330	.859***	-.332
	ESH	-.012	-.366	-.034	-.219	-.855***	.230	-.330	1	-.321	-.542*
	RE	.066	.185	.111	.210	.342	.604*	.859***	-.321	1	.032
	REM	-.622**	-0.437	-.790***	.610**	.696**	-.754***	-.332	-.542*	.032	1
D.obscura	FL	1	.618*	.750**	-.153	.350	.666*	.769**	-.489	.426	-.589*
	FMA	.618*	1	.903***	-.021	.572*	.265	.493	-.302	-.106	-.631*
	FMB	.750**	.903***	1	-.039	.573*	.478	.713**	-.359	.080	-.757**
	AEL	-.153	-.021	-.039	1	.630*	-.371	.011	.629*	.011	.554*
	AEM	.350	.572*	.573*	.630*	1	-.072	.431	-.027	.042	.084
	EN	.666*	.265	.478	-.371	-.072	1	.864***	-.498	.802**	-.695**
	CLM	.769**	.493	.713**	.011	.431	.864***	1	-.420	.748**	-.580*
	ESH	-.489	-.302	-.359	.629*	-.027	-.498	-.420	1	-.281	.468
	RE	.426	-.106	.080	.011	.042	.802**	.748**	-.281	1	-.138
	REM	-.589*	-.631*	-.757**	.554*	.084	-.695**	-.580*	.468	-.138	1
D.portschinskii	FL	1	.436	.851***	.307	.485	.234	.560*	-.382	-.034	-.356
	FMA	.436	1	.549*	.416	.531*	.102	.522*	-.331	-.011	-.129
	FMB	.851***	.549*	1	.432	.607*	.165	.610*	-.459	-.077	-.363
	AEL	.307	.416	.432	1	.839***	-.296	.403	-.526*	.149	.513*
	AEM	.485	.531*	.607*	.839***	1	-.205	.637**	-.835***	.260	.482
	EN	.234	.102	.165	-.296	-.205	1	.608*	.244	.621*	-.491
	CLM	.560*	.522*	.610*	.403	.637**	.608*	1	-.538*	.710**	.014
	ESh	-.382	-.331	-.459	-.526*	-.835***	.244	-.538*	1	-.294	-.515*
	RE	-.034	-.011	-.077	.149	.260	.621*	.710**	-.294	1	.359
	REM	-.356	-.129	-.363	.513*	.482	-.491	.014	-.515*	.359	1
D.valentini	FL	1	.565*	.755**	.273	-.061	.543*	.335	.243	-.025	-.314
	FMA	.565*	1	.851***	.135	.106	.706**	.678**	-.015	.363	-.189
	FMB	.755***	.851***	1	.022	-.111	.854***	.554*	.168	.131	-.427
	AEL	.273	.135	.022	1	.343	-.263	-.037	.105	-.043	.338
	AEM	-.061	.106	-.111	.343	1	-.485	.506	-.830***	.704**	.936***
	EN	.543*	.706**	.854***	-.263	-.485	1	.434	.309	.035	-.742**
	CLM	.335	.678**	.554*	-.037	.506	.434	1	-.658**	.888***	.214
	ESH	.243	-.015	.168	.105	-.830***	.309	-.658**	1	-.895***	-.762**
	RE	-.025	.363	.131	-.043	.704**	.035	.888***	-.895***	1	.533*
	REM	-.314	-.189	-.427	.338	.936***	-.742**	.214	-.762**	.533*	1

* FL - body length of a female, FMB and FMA - female weight before and after the egg deposition, AEL – average egg length, CLM – total mass of the eggs, RE - reproductive effort, EN – egg number, AEM – average egg mass, REM - relative egg mass (proportion of average egg mass to FMB), ESH – egg shape

(1968) proposed "weed hypothesis", explaining the distribution of parthenogenetic *Aspidoscelis* and their parental species. Unisexual *Aspidoscelis* are common in the disturbed, quickly changing habitats, and hence the parthenogens "weed" similar to plants which quickly populate the disturbed areas (Baker, 1974; Schall, 1978). In contrast, bisexual species prefer habitats with more stable environments. If we consider unisexual species as "weed" animals, we should expect that the environment they occupy is less stable than the environment of the bisexual species with similar ecology, and hence, they should possess *r* reproductive strategy compared to their parental bisexual forms. We expect that, in comparison to the bisexual species, single reproductive effort of the parthenogens and relative egg number should be higher (Schall, 1978).

Indeed, *D. armeniaca* from the studied populations invests relatively more resources into a single reproduction than the *D. valentini*, and we associate this with its common presence in less stable environments than the latter species. In contrast to the system *D. armeniaca* - *D. valentini*, parthenogenetic *D. dahli* does not invest more resources in a single reproduction than its paternal species, *D. portschinskii*. However, in *D. dahli* egg number in a clutch (but not egg size) significantly increases with female body size, whereas in *D. portschinskii* female size leads to the growth of egg size. That means, although the bisexual species does not

Table 5
Summary of a number of eggs per clutch and egg diameter of six species of *Darevskia*.

Parameter	Authors	Darevsky	Galoyan	Galoyan et al.	This Study	Se-MDE
	Year	1967	2011	2019	2022	
CNEC	*D.armeniaca*	2–5	>2-5	6	2–6	–
	D.valentini	5	–	–	2–6	–
	D.obscura	–	–	–	2–5	–
	D.dahli	2–5	–	–	1–4	–
	D.portschinskii	2–5	–	–	1–3	–
MDE	*D.armeniaca*	12–12.5	–	–	13.5	0.0205
	D.valentini	>14	–	–	14.2	0.0333
	D.obscura	12–12.5	–	–	14.05	0.0224
	D.dahli	12–12.5	–	–	14.50	0.0298
	D.portschinskii	12–12.5	–	–	16.35	0.0401

CNEC – counted number of Eggs per clutch; MDE – maximum diameter of eggs (in mm); Se-MDE – Standard error of maximum egg diameter in this study.

invest less resources in a single reproduction than its parthenogenetic daughter form, it invests more resources in producing more viable offspring, whereas the parthenogen produces more offspring at the expense of their potential viability. This correlation suggests a more stable environment for juveniles of *D. portschinskii* than that of its daughter parthenogen.

Our study supports the “weed hypothesis”, but a more unstable environment of the parthenogens may cause either spending more resources for reproduction (long-term adaptation), or in producing relatively heavier eggs (short-term adaptation to unstable juvenile environment). The particular way of *r/K* divergence between a parthenogen and its paternal species depends on the habitat type and, probably, developmental constraints related to body size. *D. dahli* may not be able to increase reproductive effort above a certain threshold because of energetic limitations related to small body size, although they favor from producing more, even lighter, eggs than *D. portschinskii*.

D. obscura, a bisexual species not parental to the studied parthenogens, invests relatively more resources in a single reproduction than *D. valentini* in a habitat where it coexists with *D. armeniaca*. This observation may suggest that the clear separation between the *r* - and *K* - reproductive strategy is easier to infer between closely related species (such as a parthenogen and its parental form) than in more phylogenetically distant ones, and if less related species are compared, species-specific habitat distribution and other ecological features may shade the effect of habitat stability on reproductive strategy.

The reason for this lineage-specific divergence pattern includes multiple factors influencing reproductive parameters, different from habitat stability. This includes the effect of body size, and related phenotypic constraints. Growth of body size in colder climates reflects Bergmann’s rule that in some cases applies to squamate reptiles (Olalla-Tárraga et al., 2006; Pincheira-Donoso et al., 2008) and hence, it explains larger bodies of *D. armeniaca* - *D. valentini* pair related to *D. dahli* - *D. portschinskii* pair. Clutch mass and reproductive effort of the large-bodied species, both sexually reproducing *D. valentini* and parthenogenetic *D. armeniaca*, is significantly larger than that of *D. portschinskii* and *D. dahli* respectively; egg size increased with reproductive effort in *D. valentini* and *D. armeniaca* but decreased in *D. portschinskii* and *D. dahli*. Besides, eggs of big-bodied species are more round in shape, whereas the eggs of *D. portschinskii* and *D. dahli* are rather elongated, although average egg mass and reproductive effort do not differ significantly among the species, with the exception of *D. armeniaca*. These facts indicate that small-bodied cannot invest so much resources into a single reproduction as larger-bodied ones, probably because of too high risk of female death associated with a high reproductive expenditures. The individuals with a larger body can deposit more eggs than small-bodied ones, without increasing reproductive effort too much.

Egg size is less dependent on female size than egg number in the studied group. We suppose this is related to a minimum threshold size that allows the eggs of *Darevskia* to develop and a maximum size of egg that female can successfully produce. The egg laying process is supposedly less traumatic for larger lizards. Vitt and Congdon (1978), Shine (1992) and Du et al. (2005) all suggest that maternal abdominal volume is an important factor limiting clutch size (and egg size) of a reptile of a given body size and shape. The eggs of small-bodied *D. dahli* and *D. portschinskii* are more elongated than this in a large-bodied species, allowing very small lizards to deposit relatively large eggs and hence ensure sufficiently high juvenile survival.

Some previous authors did not find any differences in reproductive characteristics of parthenogens and their sexually breeding relatives in nature. Schall (1978) found that clutch size, egg size and reproductive effort in *Cnemidophorus* (*Aspidoscelis*) are closer between unisexual species and their bisexual ancestors than between different species with the same reproductive mode. Menezes and Rocha (2014) did not find the differences in reproductive characteristics between four bisexuals (*Ameivula ocellifera, A. abaetensis, A. nativo, A. gulalittoralis*) and one parthenogenetic (*Cnemidophosus lacertoides*) species from the eastern Brazil. We suppose that, in the differences between the parthenogens and bisexual species do exist, however, the patterns of the differences vary from case to case, dependent on the ecological characteristics of a taxon.

Constraints related to unacceptable energy loss during single reproduction plausibly explain negative correlation of egg number with both absolute and relative egg size. Gaining of mass and energy during growth of a female is transformed into the increasing egg number. This process is discrete and not gradual, and if there is a threshold mass that triggers development of an additional egg (Ljungström et al., 2016), the females whose mass is slightly above the threshold endure a higher mass and energy loss than those below the threshold. This may increase post-reproductive mortality of the females if a clutch size exceeded the threshold; however, the abrupt growth of energy expenditures can be smoothed if the eggs in a larger clutch are lighter.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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