Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

The evolution of sexual dimorphism in semi-fossorial lizards: a case study with *Ablepharus kitaibelii*

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Keywords
SSD; morphometrics; evolution; skink; subspecies; eggs; *Ablepharus kitaibelii*; semi-fossorial.

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Editor: Andrew Kitchener
Associate Editor: Kirsty MacLeod

Received 14 November 2024; revised 19 May 2025; accepted 6 June 2025

doi:10.1111/jzo.70040

Abstract

Sexual size dimorphism (SSD) in lizards is often explained through two main evolutionary strategies: fecundity selection in females reflected in differences in abdomen length (being bigger in females) and male–male competition reflected in differences in head and body size (greater in males). However, in lizards with fossorial lifestyles, sexual dimorphism is often lacking or reduced, likely due to the constraints imposed by burrowing. In the present study, we studied the sexual size and shape dimorphism in the small semi-fossorial skink *Ablepharus kitaibelii*. Our results show a significant size dimorphism with females being larger than males in all subspecies examined. Moreover, we found differences between sexes in both relative head and abdomen size reflecting both fecundity selection and male–male competition. Females have more elongate and wider abdomens, allowing them to carry up to 5 large eggs, whereas males have bigger heads likely related to male–male aggression and territoriality. Overall, our results suggest that despite the possible constraints imposed by burrowing, in semi-fossorial species, the SSD can evolve. Future studies on other semi-fossorial and fossorial species are needed to test the generality of these results.

Introduction

Most animals exhibit differences in body size between sexes—so-called sexual size dimorphism (SSD). SSD in animals is often explained through fecundity selection in females and competition in males (Fairbairn, 1997, 2013). Cox et al. (2003) defined two of the primary adaptive hypotheses for SSD in lizards. The first hypothesis treats sexual selection for large male size, which confers an advantage in intrasexual mate competition (intrasexual selection hypothesis). The second hypothesis predicts that the natural selection for large female size confers a fecundity advantage (fecundity advantage hypothesis). SSD can also vary among habitats (Butler et al., 2000), and in function of resource availability (Peñalver-Alcázar et al., 2019). For example, previous studies have shown that when resources are limited sexual dimorphism is reduced by limiting growth in males (Bonneaud et al., 2016). Similarly, *Anolis* lizards occupying different microhabitats differ in the degree in sexual size dimorphism (Butler et al., 2000). Moreover, because viviparous females require larger abdominal space (Braña, 1996; Meiri et al., 2020), at an intraspecific level, oviparous populations could be less female-biased in abdomen size as less space is needed for house eggs compared to developing embryos (Roitberg et al., 2020).

In many species of lizards, sexual shape dimorphism is also observed with females having larger abdomens and males having larger heads irrespective of variation in overall body size. Sexual selection via male–male combat could lead to an increase in head size (Carothers, 1984; Cox et al., 2007; Vitt & Cooper, 1985), whereas selection acting on clutch size or clutch volume in females might promote larger abdomen size (Griffith, 1991; Shine, 1989). According to Braña (1996), in adult lacertids, abdomen volume and head size increase in both sexes, but abdomen length increased at a higher rate with size in females. Cox & John-Alder (2007) further posited that SSD develops in *Sceloporus virgatus* Smith 1938 (female-larger) because females grow faster than males, particularly during the spring mating season. In contrast, SSD develops in *S. jarrovii*

Cope, 1875 (male-larger) because the males grow more quickly than females throughout the first year of life, as has also been observed for *Anolis* lizards (Bonneaud et al., 2016). In some species, sexes differ in the number of trunk vertebrae, with females having more vertebrae than males (Porkert & Grosseova, 1986). Consequently, given that selection may act specifically on the head or the trunk, measures of sexual size dimorphism based on snout-vent length may be problematic (Borczyk et al., 2014; Kratochvíl et al., 2003; Scharf & Meiri, 2013).

In Scincidae, a clade of generally elongate lizards, most sexually dimorphic traits are related to body length (elongated abdomen and more ventral scales in females; Olsson et al., 2002) and head size (being slightly bigger in males; Griffith, 1991). Interestingly, in many species of Scincidae, SSD is not clearly expressed or even lacking (Cox et al., 2007; Heideman et al., 2008). This could be related to the fossorial or semi-fossorial lifestyle of many of the species. Burrowing animals are strongly constrained in their body and head diameter as the energetic cost of burrowing increases exponentially with diameter (Navas et al., 2004). Consequently, sexual selection for enlarged head size may be countered by natural selection on the cost of burrowing. Moreover, data regarding male–male interactions are lacking for many fossorial lizards, making it difficult to ascertain the role of male–male combat in driving differences between the sexes (Heideman et al., 2008; Schwarzkopf, 2005).

An excellent model to investigate sexual dimorphism in size and shape is the semi-fossorial and small-sized scincid lizard, *Ablepharus kitaibelii*. Even if this species is semi-fossorial, we predict that the same constraints would apply, as efficient locomotion through leaf litter of the top soil may benefit from narrow heads and elongate bodies. To date, sexual dimorphism in this species has not been investigated in detail, partly due to the lack of reliable sexing methods (Jovanović-Glavaš et al., 2018; Vergilov et al., 2022). Previous studies have suggested there are no sexual differences in the coloration of this species (Gruber, 1981). The only detailed data on the body morphometrics of the Snake-eyed Skink were published by Ljubisavljević et al. (2002), Vergilov & Tzankov (2014), Jovanović-Glavaš et al. (2018), and Zimić et al. (2018), but none of these studies treated sexual dimorphism in the species. Interestingly, prolonged and aggressive combat between males of *A. kitaibelii* was observed by Teschler (1885). Moreover, limbless, tailless, and toeless individuals were described previously by Vergilov (2017) and Vergilov & Kornilev (2019). This could be explained by male–male combat, despite the fact that the species has many natural enemies, and this could expose them to predation (Vergilov, 2017). As a short-lived species that grows quickly and can become sexually mature after the first hibernation, females may grow more rapidly to accommodate the large eggs in the abdomen (Vergilov, Necheva, & Zlatkov, 2018; Vergilov, Tzankov, & Zlatkov, 2018).

In the present study, we use a comprehensive population-level dataset encompassing all four subspecies of *A. kitaibelii* across the entire distribution area to explore differences between males and females in this diminutive semi-fossorial species. We test the hypothesis that burrowing imposes constraints on sexual dimorphism. We also present data on egg number, size, and volume to explore possible fecundity selection.

Materials and methods

In the current study, we divided the specimens into the four subspecies, according to their morphology and distribution. The total number of studied specimens was 298, of which 52 *A. kitaibelii kitaibelii* (29 females and 23 males), 175 *A. k. stepaneki* (90 females and 85 males), 40 *A. k. fitzingeri* (16 females and 24 males), and 31 *A. k. fabichi* (14 females and 17 males) were retained for the statistical analysis. Specimens were from different localities in Bulgaria, Romania, Turkey, Greece, Hungary, and Albania. This included a total of 149 females and 149 males. The specimens came from the collections of the Institute of Biodiversity and Ecosystem Research at the Bulgarian Academy of Sciences (IBER-BAS), the Natural History Museum of Vienna (NHMW), and the Hungarian Natural History Museum (HNHM). The sex of the specimens was determined by dissection. The smallest adult male and female specimens had a body length of over 38 mm (see Vergilov et al., 2022; Vergilov, Necheva, & Zlatkov, 2018). Previous studies stated that the smallest specimens with fully developed reproductive organs, based on the size of the gonads determined via dissection, had a body length of 30.7 mm (Vergilov & Tzankov, 2014) and a body length of 32 mm (Ljubisavljević et al., 2002; Schmidtler, 1997).

For the statistical analyses, a total number of nine metric and four meristic traits were used (Table 1, Supporting Information Appendix S1). The snout-vent length was taken with a ruler. The other meristic traits (for the specimens from Bulgaria) were taken with a Carl Zeiss stereomicroscope SM XX (Jena). The skinks from Romania were investigated using a Leica MS5 stereomicroscope (for the specimens of the Natural History Museum of Vienna) and a Leica MZ95 stereomicroscope (for the specimens from the Hungarian Natural History Museum). Some meristic and metric traits (snout-vent length, the number of supralabial, ventral, dorsal, and nuchal scales) were measured and counted according to the methods of Schmidtler (1997). All other traits (except head width) were measured as in Ljubisavljević et al. (2002). The values from the micrometre scale were converted into millimetres with an accuracy of one hundredth of a mm. The length of the tail was not included in this study because of the low number of specimens having a full-sized tail.

All data were Log_{10}-transformed before analyses. We first tested for sexual size dimorphism using a univariate ANOVA with species and sex and the interaction as factors and Log_{10}-transformed snout-vent length as our dependent variable. We next regressed each Log_{10}-transformed morphometric trait and scale count on Log_{10}-transformed snout-vent length and saved unstandardized residuals for those traits where regressions were significant. To test for sexual shape dimorphism, we ran a MANOVA with sex and subspecies as factors and the residual traits, the number of supralabials, and the number of nuchal scales as our variables. We subsequently ran univariate

Table 1 The means and standard deviations for the different traits for the subspecies studied

		Males			Females		
Subspecies	Trait	*N*	Mean	SD	*N*	Mean	SD
A. k. stepaneki	Number of ventral scales	85	61.39	3.23	90	66.93	3.64
	Number of dorsal scales	83	19.92	0.52	89	20.08	0.68
	SVL (mm)	85	42.29	2.53	90	45.98	3.36
	Forelimb length (mm)	85	7.58	0.45	88	7.23	0.50
	Hind limb length (mm)	84	10.88	0.71	86	10.34	0.67
	Hind foot length (mm)	84	4.91	0.39	87	4.63	0.38
	Head length (mm)	84	6.31	0.30	89	6.06	0.30
	Pileus length (mm)	85	5.60	0.29	90	5.38	0.29
	Head width (mm)	84	4.32	0.29	90	4.22	0.29
	Head height (mm)	85	3.30	0.26	90	3.26	0.32
	Number of supralabials	84	6.13	0.46	89	6.09	0.39
	Number of nuchals	83	6.58	0.91	89	6.57	0.90
	Eye diameter (mm)	85	1.14	0.07	90	1.13	0.10
A. k. kitaibelii	Number of ventral scales	23	61.22	2.97	29	66.41	3.74
	Number of dorsal scales	23	19.87	0.76	29	19.90	0.41
	SVL (mm)	23	39.48	4.92	29	42.78	4.93
	Forelimb length (mm)	23	7.06	0.64	29	6.86	0.46
	Hind limb length (mm)	23	9.93	1.10	29	9.85	0.79
	Hind foot length (mm)	23	4.59	0.49	29	4.40	0.34
	Head length (mm)	23	5.95	0.59	29	5.82	0.48
	Pileus length (mm)	23	5.25	0.52	29	5.07	0.35
	Head width (mm)	23	4.04	0.47	29	3.87	0.32
	Head height (mm)	23	3.21	0.40	29	3.10	0.29
	Number of supralabials	23	6.09	0.29	29	6.03	0.19
	Number of nuchals	23	6.78	0.90	29	7.03	1.02
	Eye diameter (mm)	23	1.10	0.10	29	1.08	0.07
A. k. fitzingeri	Number of ventral scales	24	62.13	2.68	16	68.25	3.66
	Number of dorsal scales	24	19.92	1.21	16	19.69	0.87
	SVL (mm)	24	40.07	2.19	16	44.89	5.05
	Forelimb length (mm)	24	7.20	0.49	16	7.17	0.60
	Hind limb length (mm)	24	10.49	0.78	16	10.07	0.80
	Hind foot length (mm)	24	4.78	0.49	16	4.63	0.49
	Head length (mm)	24	6.01	0.31	16	5.93	0.31
	Pileus length (mm)	24	5.44	0.27	16	5.27	0.33
	Head width (mm)	24	3.97	0.28	16	3.91	0.30
	Head height (mm)	24	3.22	0.27	16	3.21	0.35
	Number of supralabials	24	6.42	0.72	16	6.19	0.40
	Number of nuchals	24	7.13	1.68	16	7.25	1.18
	Eye diameter (mm)	24	1.12	0.09	16	1.34	0.84
A. k. fabichi	Number of ventral scales	17	62.29	3.35	14	65.57	2.56
	Number of dorsal scales	17	19.76	0.56	14	19.79	0.58
	SVL (mm)	17	41.22	3.74	14	42.00	4.83
	Forelimb length (mm)	17	8.94	0.63	14	8.33	0.51
	Hind limb length (mm)	17	13.49	1.09	14	12.55	0.85
	Hind foot length (mm)	17	6.32	0.45	14	5.87	0.47
	Head length (mm)	17	6.77	0.46	14	6.34	0.37
	Pileus length (mm)	17	5.87	0.38	14	5.58	0.33
	Head width (mm)	17	4.27	0.42	14	4.28	0.50
	Head height (mm)	17	3.67	0.19	14	3.62	0.29
	Number of supralabials	17	6.24	0.56	14	6.57	0.94
	Number of nuchals	17	8.06	1.03	14	7.93	1.59
	Eye diameter (mm)	17	1.23	0.09	14	1.47	1.08

ANOVAs for each trait to test for differences between sexes, subspecies, and the interaction. As interaction effects were not significant, we then ran Bonferroni post-hoc tests to test which subspecies were different from one another. Statistics were performed using IBMSPSS (V. 29, Armonk, NY, USA).

Eggs were laid by specimens held in captivity (in 2011, 2012 and 2016) from three Bulgarian localities (the UTM grid squares 10 × 10 km of the localities are given in brackets) – Pchelin Village (MH84), Razdel Village (MG75) and from the touristic road Brodilovo-Ahtopol (NG75). Two females from Brodilovo-Ahtopol laid 10 eggs (five eggs for each individual), one female from Razdel laid three eggs, and three females from Pchelin laid 10 eggs together in one box with coconut substrate (three were found dehydrated on the next day). Two of the females from Pchelin laid four eggs each, and one laid only two. The incubation was accomplished at room temperature, with eggs buried in a coconut substrate inside plastic boxes (500–800 mL). Each egg was measured (until the fifth day after laying) by electronic callipers with an accuracy of 0.01 mm. The form of the eggs was ellipsoidal, so the volume of the eggs (in mm^3) was calculated by the volume of an ellipsoid: $V = 4/3\ \pi\ (R_1/2)\ (R_2/2)^2$, where R_1 is the length of the long axis and R_2—diameter of the ellipsoid.

Results

The means and standard deviations for the different traits for the subspecies studied are provided in Table 1. The ANOVA testing for sexual size dimorphism showed significant differences in snout-vent length between sexes ($F_{1,290} = 33.43$; $P < 0.001$) and subspecies ($F_{3,290} = 12.85$; $P < 0.001$) but no interaction effects ($F_{3,290} = 1.76$; $P = 0.16$). In all subspecies, females were larger than males. Post-hoc tests further showed that *A. k. stepaneki* was significantly larger than the other subspecies (all $P < 0.05$). However, none of the other subspecies differed from one another in snout-vent length.

The MANOVA testing for sexual shape dimorphism detected significant sex (Wilks' lambda = 0.60; $F_{12,271} = 14.79$; $P < 0.001$) and subspecies (Wilks' lambda = 0.22; $F_{36,801} = 14.98$; $P < 0.001$) effects but no interactions (Wilks' lambda = 0.84; $F_{36,801} = 1.36$; $P = 0.079$). Subsequent univariate ANOVAs detected significant sex effects for all variables except the number of supralabials, the number of nuchals, the residual number of dorsal scales, and the residual eye diameter (Table 2). Males were larger in all dimensions when controlling for variation in snout-vent length except for the number of ventral scales, which were larger in females.

Subspecies effects were significant for all traits with the exception of the residual number of dorsal scales (Table 2). Post-hoc tests indicated that all four subspecies were well differentiated based on the morphological and meristic traits except for the residual number of dorsal and ventral scales (Table 3).

The data from the egg measurements are presented in Table 4. Eggs had a size of 10 mm in length, 5.5–6 mm in diameter, and a volume between 163.23 and 322.93 mm^3. The body length of the female from Razdel was 56.5 mm, with a mean egg length of 9.91 mm and a mean egg diameter of 4.8 mm. The three eggs also had the same volume and weight. Only one of the two females from Brodilovo-Ahtopol and two of the three females from Pchelin were measured. The body lengths of the females from Brodilovo-Ahtopol and Pchelin were: Brodilovo-Ahtopol female—51 mm; Pchelin females—46.9 and 47 mm. The individuals from Brodilovo-Ahtopol (in one box) and from Pchelin (in other box) laid eggs together, so it is not possible to say which egg belongs to which female. When measuring the Bulgarian specimens, it was observed that some large females can hold up to five eggs in their abdomens. Most of them, however, held three or four eggs (see Fig. 1; see Vergilov, Necheva, & Zlatkov, 2018; Vergilov, Tzankov, & Zlatkov, 2018).

Table 2 Results from the univariate ANOVAs testing for differences between sexes and subspecies

	d.f.	*F*	*P*
Sex			
# supralabial scales	1282	0.010	0.921
# nuchal scales	1282	0.164	0.685
Residual forelimb length	1282	54.373	<**0.001**
Residual hind limb length	1282	48.867	<**0.001**
Residual foot length	1282	29.912	<**0.001**
Residual head length	1282	100.308	<**0.001**
Residual pileus length	1282	98.814	<**0.001**
Residual head width	1282	28.229	<**0.001**
Residual head depth	1282	10.150	**0.002**
Residual # ventral scales	1282	61.516	<**0.001**
Residual # dorsal scales	1282	0.439	0.508
Residual eye size	1282	0.048	0.826
Subspecies			
# supralabial scales	3282	5.662	<**0.001**
# nuchal scales	3282	16.188	<**0.001**
Residual forelimb length	3282	101.854	<**0.001**
Residual hind limb length	3282	133.485	<**0.001**
Residual foot length	3282	100.777	<**0.001**
Residual head length	3282	44.202	<**0.001**
Residual pileus length	3282	32.642	<**0.001**
Residual head width	3282	17.731	<**0.001**
Residual head depth	3282	22.656	<**0.001**
Residual # ventral scales	3282	2.993	**0.031**
Residual # dorsal scales	3282	1.034	0.378
Residual eye size	3282	12.034	<**0.001**

Bold values indicate significant differences.
d.f., degrees of freedom.

Discussion

Sexual size and shape dimorphism in *A. kitaibelii*

The Snake-eyed Skink is a species with subtle differences between both sexes (Jovanović-Glavaš et al., 2018; Ljubisavljević et al., 2002; Vergilov et al., 2022). Previous ecological studies, including field morphological measurements, have outlined the difficulty of sexing individuals, mostly ones with overlapping sizes—before and shortly after maturation

Table 3 Results of the Bonferroni post-hoc tests exploring which variables discriminate between the different subspecies

	Mean Difference	SE	*P*
# supralabials			
A. k. fabichi			
A. k. fitzingeri	0.0034	0.0071	1.000
A. k. kitaibelii	0.021	0.0067	**0.014**
A. k. stepaneki	0.018	0.0058	**0.012**
A. k. fitzingeri			
A. k. fabichi	−0.0034	0.0071	1.000
A. k. kitaibelii	0.017	0.0062	**0.035**
A. k. stepaneki	0.015	0.0052	**0.032**
A. k. kitaibelii			
A. k. fabichi	−0.021	0.0067	**0.014**
A. k. fitzingeri	−0.017	0.0062	**0.035**
A. k. stepaneki	−0.0026	0.0047	1.000
A. k. stepaneki			
A. k. fabichi	−0.018	0.0058	**0.012**
A. k. fitzingeri	−0.015	0.0052	**0.032**
A. k. kitaibelii	0.0026	0.0047	1.000
# nuchals			
A. k. fabichi			
A. k. fitzingeri	0.050	0.016	**0.009**
A. k. kitaibelii	0.062	0.015	<**0.001**
A. k. stepaneki	0.086	0.013	<**0.001**
A. k. fitzingeri			
A. k. fabichi	−0.050	0.016	**0.009**
A. k. kitaibelii	0.012	0.014	1.000
A. k. stepaneki	0.036	0.012	**0.013**
A. k. kitaibelii			
A. k. fabichi	−0.062	0.015	<**0.001**
A. k. fitzingeri	−0.012	0.014	1.000
A. k. stepaneki	0.024	0.010	0.135
A. k. stepaneki			
A. k. fabichi	−0.086	0.013	<**0.001**
A. k. fitzingeri	−0.036	0.012	**0.013**
A. k. kitaibelii	−0.024	0.010	0.135
Residual forelimb length			
A. k. fabichi			
A. k. fitzingeri	0.083	0.0059	<**0.001**
A. k. kitaibelii	0.095	0.0056	<**0.001**
A. k. stepaneki	0.077	0.0048	<**0.001**
A. k. fitzingeri			
A. k. fabichi	−0.083	0.0059	<**0.001**
A. k. kitaibelii	0.012	0.0052	0.125
A. k. stepaneki	−0.0054	0.0043	1.000
A. k. kitaibelii			
A. k. fabichi	−0.095	0.0056	<**0.001**
A. k. fitzingeri	−0.012	0.0052	0.125
A. k. stepaneki	−0.017	0.0039	<**0.001**
A. k. stepaneki			
A. k. fabichi	−0.077	0.0048	<**0.001**
A. k. fitzingeri	0.0054	0.0043	1.000
A. k. kitaibelii	0.017	0.0039	<**0.001**
Residual hind limb length			
A. k. fabichi			
A. k. fitzingeri	0.10	0.0066	<**0.001**
A. k. kitaibelii	0.12	0.0063	<**0.001**
A. k. stepaneki	0.10	0.0054	<**0.001**
A. k. fitzingeri			
A. k. fabichi	−0.10	0.0066	<**0.001**
A. k. kitaibelii	0.017	0.0058	**0.023**
A. k. stepaneki	−0.0048	0.0049	1.000
A. k. kitaibelii			
A. k. fabichi	−0.12	0.0063	<**0.001**
A. k. fitzingeri	−0.017	0.0058	**0.023**
A. k. stepaneki	−0.022	0.0044	<**0.001**
A. k. stepaneki			
A. k. fabichi	−0.099	0.0054	<**0.001**
A. k. fitzingeri	0.0048	0.0049	1.000
A. k. kitaibelii	0.022	0.0044	<**0.001**
Residual foot length			
A. k. fabichi			
A. k. fitzingeri	0.11	0.0086	<**0.001**
A. k. kitaibelii	0.13	0.0081	<**0.001**
A. k. stepaneki	0.11	0.0070	<**0.001**
A. k. fitzingeri			
A. k. fabichi	0–0.11	0.0086	<**0.001**
A. k. kitaibelii	0.020	0.0075	**0.042**
A. k. stepaneki	−0.00042	0.0063	1.000
A. k. kitaibelii			
A. k. fabichi	−0.13	0.0081	<**0.001**
A. k. fitzingeri	−0.020	0.0075	**0.042**
A. k. stepaneki	−0.021	0.0057	**0.002**
A. k. stepaneki			
A. k. fabichi	−0.11	0.0070	<**0.001**
A. k. fitzingeri	0.00042	0.0063	1.000
A. k. kitaibelii	0.021	0.0057	**0.002**
Residual head length			
A. k. fabichi			
A. k. fitzingeri	0.043	0.0044	<**0.001**
A. k. kitaibelii	0.048	0.0042	<**0.001**
A. k. stepaneki	0.037	0.0036	<**0.001**
A. k. fitzingeri			
A. k. fabichi	−0.043	0.0044	<**0.001**
A. k. kitaibelii	0.0055	0.0039	0.978
A. k. stepaneki	−0.0057	0.0033	0.488
A. k. kitaibelii			
A. k. fabichi	−0.048	0.0042	<**0.001**
A. k. fitzingeri	−0.0055	0.0039	0.978
A. k. stepaneki	−0.011	0.0029	**0.001**
A. k. stepaneki			
A. k. fabichi	−0.037	0.0036	<**0.001**
A. k. fitzingeri	0.0057	0.0033	0.488
A. k. kitaibelii	0.011	0.0029	**0.001**
Residual pileus length			
A. k. fabichi			
A. k. fitzingeri	0.030	0.0047	<**0.001**
A. k. kitaibelii	0.046	0.0044	<**0.001**
A. k. stepaneki	0.029	0.0038	<**0.001**
A. k. fitzingeri			
A. k. fabichi	−0.030	0.0047	<**0.001**
A. k. kitaibelii	0.016	0.0041	<**0.001**
A. k. stepaneki	−0.0016	0.0034	1.000
A. k. kitaibelii			
A. k. fabichi	−0.046	0.0044	<**0.001**

Table 3 Continued.

	Mean Difference	SE	*P*
A. k. fitzingeri	−0.016	0.0041	**<0.001**
A. k. stepaneki	−0.018	0.0031	**<0.001**
A. k. stepaneki			
A. k. fabichi	−0.029	0.0038	**<0.001**
A. k. fitzingeri	0.0016	0.0034	1.000
A. k. kitaibelii	0.018	0.0031	**<0.001**
Residual head width			
A. k. fabichi			
A. k. fitzingeri	0.035	0.0069	**<0.001**
A. k. kitaibelii	0.033	0.0065	**<0.001**
A. k. stepaneki	0.011	0.0056	0.370
A. k. fitzingeri			
A. k. fabichi	−0.035	0.0069	**<0.001**
A. k. kitaibelii	−0.0022	0.0061	1.000
A. k. stepaneki	−0.025	0.0051	**<0.001**
A. k. kitaibelii			
A. k. fabichi	−0.033	0.0065	**<0.001**
A. k. fitzingeri	0.0022	0.0061	1.000
A. k. stepaneki	−0.023	0.0046	**<0.001**
A. k. stepaneki			
A. k. fabichi	−0.011	0.0056	0.370
A. k. fitzingeri	0.025	0.0051	**<0.001**
A. k. kitaibelii	0.023	0.0046	**<0.001**
Residual head depth			
A. k. fabichi			
A. k. fitzingeri	0.057	0.0087	**<0.001**
A. k. kitaibelii	0.065	0.0082	**<0.001**
A. k. stepaneki	0.054	0.0071	**<0.001**
A. k. fitzingeri			
A. k. fabichi	−0.057	0.0087	**<0.001**
A. k. kitaibelii	0.0074	0.0076	1.000
A. k. stepaneki	−0.0034	0.0064	1.000
A. k. kitaibelii			
A. k. fabichi	−0.065	0.0082	**<0.001**
A. k. fitzingeri	−0.0074	0.0076	1.000
A. k. stepaneki	−0.011	0.0058	0.365
A. k. stepaneki			
A. k. fabichi	−0.054	0.0071	**<0.001**
A. k. fitzingeri	0.0034	0.0064	1.000
A. k. kitaibelii	0.011	0.0058	0.365
Residual # ventral scales			
A. k. fabichi			
A. k. fitzingeri	−0.0040	0.0055	1.000
A. k. kitaibelii	−0.0030	0.0052	1.000
A. k. stepaneki	0.0042	0.0045	1.000
A. k. fitzingeri			
A. k. fabichi	0.0040	0.0055	1.000
A. k. kitaibelii	0.0010	0.0048	1.000
A. k. stepaneki	0.0081	0.0040	0.269
A. k. kitaibelii			
A. k. fabichi	0.0030	0.0052	1.000
A. k. fitzingeri	−0.0010	0.0048	1.000
A. k. stepaneki	0.0071	0.0036	0.310
A. k. stepaneki			
A. k. fabichi	−0.0042	0.0045	1.000
A. k. fitzingeri	−0.0081	0.0040	0.269
A. k. kitaibelii	−0.0071	0.0036	0.310
Residual # dorsal scales			
A. k. fabichi			
A. k. fitzingeri	−0.00047	0.0036	1.000
A. k. kitaibelii	−0.0026	0.0034	1.000
A. k. stepaneki	−0.0037	0.0029	1.000
A. k. fitzingeri			
A. k. fabichi	0.00047	0.0036	1.000
A. k. kitaibelii	−0.0021	0.0031	1.000
A. k. stepaneki	−0.0032	0.0026	1.000
A. k. kitaibelii			
A. k. fabichi	0.0026	0.0034	1.000
A. k. fitzingeri	0.0021	0.0031	1.000
A. k. stepaneki	−0.0011	0.0024	1.000
A. k. stepaneki			
A. k. fabichi	0.0037	0.0029	1.000
A. k. fitzingeri	0.0032	0.0026	1.000
A. k. kitaibelii	0.0011	0.0024	1.000
Residual eye size			
A. k. fabichi			
A. k. fitzingeri	0.041	0.013	**0.014**
A. k. kitaibelii	0.066	0.013	**<0.001**
A. k. stepaneki	0.061	0.011	**<0.001**
A. k. fitzingeri			
A. k. fabichi	−00.041	0.013	**0.014**
A. k. kitaibelii	0.025	0.012	0.228
A. k. stepaneki	0.019	0.0099	0.303
A. k. kitaibelii			
A. k. fabichi	−0.066	0.013	**<0.001**
A. k. fitzingeri	−0.025	0.012	0.228
A. k. stepaneki	−0.0052	0.0089	1.000
A. k. stepaneki			
A. k. fabichi	−0.061	0.011	**<0.001**
A. k. fitzingeri	−0.019	0.0099	0.303
A. k. kitaibelii	0.0052	0.0089	1.000

Bolded values represent significant differences between subspecies.

(Jovanović-Glavaš et al., 2018; Vergilov et al., 2022). Observations in the field confirmed that some individuals express orange colouration on the ventral side of the body, but the belly colour is not related to a particular sex (Jovanović-Glavaš et al., 2018; personal observations).

Other external traits, used also as a base for taxonomical differentiation, overlap and are influenced by ecological factors (Vergilov & Tzankov, 2014). Our results reveal that (1) females are significantly larger than males in snout-vent length, and (2) that males are significantly larger in most dimensions when correcting for variation in snout-vent length. Sexes differ in most traits, except the number of supralabials, the number of nuchals (which can vary from 4 to 13, but mostly between 6 and 8), the residual number of dorsal scales, and the residual eye diameter (Table 2). These data confirm that the main dimorphic traits in the species are body length and head dimensions (Jovanović-Glavaš et al., 2018; Ljubisavljević et al., 2002; Vergilov & Tzankov, 2014). Supralabial scales in some individuals may differ on both sides of the upper jaw—3 scales on one side and 4 on the other (Fig. 2).

Table 4 Descriptive statistics (*n* - number of eggs; mean ± SD; Min–Max) of the eggs of *A. kitaibelii*

Locality	R_1	R_2	mm^3
Pchelin	*n* = 7 10.94 ± 0.91 (9.85–12.33)	*n* = 7 6.74 ± 0.54 (5.98–5.73)	*n* = 7 261.00 ± 41.22 (184.34–322.93)
Brodilovo –Ahtopol	*n* = 10 10.13 ± 0.74 (9.10–11.11)	*n* = 10 6.16 ± 0.25 (5.73–6.55)	*n* = 10 201.29 ± 19.99 (163.23–224.97)
Razdel	*n* = 3 9.91 ± 0.53 (9.31–10.32)	*n* = 3 4.8 ± 0.15 (4.66–4.95)	*n* = 3 119.14 ± 1.76 (117.28–120.77)

mm^3, volume of the eggs; R_1, length of the long axis, R_2, diameter of the ellipsoid.

Figure 1 Disposition of 4 eggs (first two photos) and 5 eggs (third photo) in female specimens from Bulgaria.

When comparing subspecies, our data confirm some previous observations but also question the main traits typically used as taxonomic proxies to establish differences. For example, the number of dorsal scales (around midbody) was previously used for taxonomical differentiation between subspecies (Fuhn, 1970; Schmidtler, 1997). Our analyses and observations contradict these statements, as no statistically significant differences were found in this trait. Moreover, Ljubisavljević et al. (2002) revealed that there is evidence of hybridisation in intergradation zones where different subspecies are co-occurring, showing that in some populations there is an overlap between individuals in the number of dorsal scales, and that there is no significant geographic variation in this trait. Other authors have stated that the number of dorsals was not different between *A. k. kitaibelii* and *A. k. stepaneki*. Regarding the other dimensions in this study, the subspecies remain well-defined, which can be explained by the different habitats they are adapted to or their isolation, like for *A. k. fabichi* on some Greek islands (see Štepánek, 1937 for *A. k. fabichi*). Fuhn (1970) & Gruber (1981) described the differences in the external body dimensions between different populations on the Balkan and Aegean Islands (southern and northern). Later, Schmidtler (1997) gave a diagnosis for the different subspecies of *A. kitaibelii*, mainly focusing on the head and body size differences, colouration, and head and body pholidosis. The phylogenetic relationships between subspecies have not been described to this date, preventing us from taking them into account in our analyses.

Interestingly, based on the limited knowledge about the behavior of the species, it has been suggested that males do not show territorial defense, neither in captivity nor in the wild. Indeed, Gruber (1981) stated that the Snake-eyed Skink is not a territorial species, in accordance with previous publications on the species describing *A. kitaibelii* as non-territorial and having a secretive lifestyle. Yet, our results showed a distinct head shape dimorphism. Moreover, Teschler (1885) observed a combat between male individuals, biting each other on the body. Such combats could cause serious damage, as observed in natural populations and under laboratory conditions (Jovanović-Glavaš et al., 2018; Vergilov, 2017; Vergilov & Kornilev, 2019). The exposure to predation in open areas while fighting during the mating season could, moreover, potentially be fatal, considering the large number of predators inhabiting the ecotones where the species can be found (Gruber & Fuchs, 1977; Rotter, 1962; Vergilov, 2017; Vergilov & Kornilev, 2019; Zimić et al., 2018).

Reproductive investment in *A. kitaibelii*

Because of its tiny size (Jovanović-Glavaš et al., 2018; Ljubisavljević et al., 2002; Vergilov & Tzankov, 2014; Zimić et al., 2018; this study), *A. kitaibelii* lays a small number of eggs – according to our observations, between one and five based on observations of live animals and dissected specimens (Fig. 1). Other authors reported the same number of eggs for the species, namely two to four (Beshkov & Nanev, 2006; Garbov, 1990; Jovanović-Glavaš et al., 2018; Valakos

Figure 2 Individual with different numbers of supralabials on both sides of the upper jaw.

et al., 2008; Vergilov, Necheva, & Zlatkov, 2018) and two to five (Fuhn, 1970). This is characteristic for many other minute lizards with a secretive lifestyle (see Shine & Greer, 1991). According to our results, the eggs in *A. kitaibelii* are very large compared to the body of the females. Females are larger than males, likely to accommodate the eggs in the body cavity. The eggs are positioned inside the body in a zig-zag pattern, with each egg partially overlapping (Fig. 1). The placement of the eggs shifts some of the internal organs, for example, the lungs are folded upwards to the anterior part of the body and the guts are bent between the eggs (Fig. 1). All these anatomical changes are probably related with the more rapid growth in females than males at the beginning of sexual maturity (Vergilov, Tzankov, & Zlatkov, 2018). It is also probable that because of the large size of the eggs in comparison to the size of the females (see also Fig. 1a in Vergilov & Natchev, 2018) that females would need more energy during the reproductive season. This is probably why the females of this species produce only one clutch of eggs. The period of egg-laying is extended between 1 to 2 months (Valakos et al., 2008; Vergilov, Necheva, & Zlatkov, 2018) or up to 3 months depending on the climatic conditions (Stojanov et al., 2011). Though some population variation in the egg-laying period and the period of the incubation between different populations, northern and southern, exists (Jovanović-Glavaš et al., 2018; Vergilov, Necheva, & Zlatkov, 2018), females from all populations likely only lay one clutch, similar to other representatives of the genus (Göçmen et al., 1996; Goldberg, 2012).

In the Snake-eyed Skink, females possess significantly longer and more elongated bodies than males (Jovanović-Glavaš et al., 2018; Ljubisavljević et al., 2002; Vergilov, Tzankov, & Zlatkov, 2018). This strategy is likely related to the growth of the eggs in the bodies of the females. According to Jovanović-Glavaš et al. (2018), the size of the *A. kitaibelii* females is not related to the number of eggs but only to the size of the eggs inside the females. Our personal data are not conclusive on this matter. According to Goldberg (2012), the smaller species, *A. rueppellii*, lays a smaller number of eggs (three). The volume of the eggs of the Snake-eyed Skink is very large; our results reveal that the eggs had a volume between 119.14 and 261.00 mm^3 (mean values), while those of Jovanović-Glavaš et al. (2018) had a mean volume of 148.92 mm^3. Rotter (1962) measured eggs of the species and provided data about their growth. The author stated that the eggs were 7.1–7.2 mm long after laying; 11 mm on the 21st day; 12.1 mm on the 27th day, and 13.8 mm on 37th day. Garbov (1990) gives the only data from Bulgaria about the reproduction of the skink and revealed that one individual in captivity laid four eggs: app. 1 cm long and 0.5 cm wide, similar to data presented by Jovanović-Glavaš et al. (2018) – 9.84 mm (mean length) and 5.34 mm (mean width). Although our dataset is limited, published data and our observations hint at the fact that smaller females cannot produce more than three to four eggs, contrary to the larger ones which can produce four to five eggs. Moreover, egg volume appears similar and independent of the size of the female. Thus, the assumption of Vergilov, Necheva, and Zlatkov (2018) suggesting that female body size is related to the number of eggs appears valid.

Sexual size and shape dimorphism in scincid lizards

Scincids are an interesting group of highly diverse lizards, often with secretive lifestyles. Possibly because of their secretive lifestyle, studies on sexual dimorphism are relatively scant. Here, we summarize studies on sexual size and shape dimorphism in the group (see Table 5) and show that in the majority of cases, male-biased sexual shape dimorphism in head dimensions was observed in terrestrial lizards. Interestingly, a study on members of the legless subfamily Acontiinae (genera *Acontias*, *Microacontias*, *Acontophiops* and *Typhlosaurus*) revealed head shape dimorphism only in a small subset of the taxa investigated (3 of 10 species) and size dimorphism only in two species (Heideman et al., 2008; Table 5). This suggests that size and head shape dimorphism may be strongly reduced in fossorial animals, possibly due to the morphological adaptations for a burrowing lifestyle (Gans, 1978) and the high cost of burrowing that increases exponentially with head diameter (Navas et al., 2004). In the African caecilian *Schistometopum thomense* (Bocage, 1873), however, head shape does differ between the sexes, with males having larger and blunter heads compared to females (Teodecki et al., 1998). However, this is a largely surface-dwelling species that may indeed be less constrained in the development of head shape dimorphism. Interestingly, our data suggest that semi-fossorial lizard species like *A. kitaibelii* may also be less constrained and consequently

Table 5 Studies regarding shape and size dimorphism in members of family Scincidae

Studies	Genus/Species/ Subspecies	SSD	SShD	Body dimentions (shape and size)
Fossorial				
Heideman et al. (2008)	*Acontias g. gracilicauda*	Female-biased		Females having bigger bodies than males
Heideman et al. (2008)	*Acontias m. meleagris*	Male-biased	Male-biased	Males possesing larger bodies than females; males having significantly larger heads than females
Heideman et al. (2008)	*Acontias m. orientalis*	Female-biased		Females having bigger bodies than males
Heideman et al. (2008)	*Acontias m. orientalis (lineicauda morph)*	Female-biased		Females having bigger bodies than males
Heideman et al. (2008)	*Acontias percivali*	Female-biased		Females having slighter bigger bodies than males
Heideman et al. (2008)	*Acontias p. occidentalis*	Male-biased	Male-biased	Males are larger than females; males having significantly larger heads than females
Heideman et al. (2008)	*Acontias p. tasmani*	Male-biased		Males are slightly larger than females
Heideman et al. (2008)	*Acontophiops lineatus*	Female-biased		Females having bigger bodies than males
Heideman et al. (2008)	*Microacontias litoralis*	None	Male-biased	No significant difference between SVL of males and females; males having significantly larger heads than females
Heideman et al. (2008)	*Typhlosaurus vermis*	Male-biased		Males are slightly larger than females;
Semi-fossorial				
Becker & Paulissen (2012)	*Scincella lateralis*	Female-biased	Male-biased	Longer, wider and deeper heads in males; females slightly larger than males
Clemann et al. (2004)	*Lissolepis coventryi*	None	Male-biased	Males have larger heads (in absolute size and head size relative to body size); both sexes do not differ in body size
Du & Ji (2001); Zhang & Ji (2004)	*Plestiodon elegans*	Male-biased	Male-biased	Larger heads and longer bodies in males
Dubey et al. (2011)	*Eulamprus leuraensis*	None	Male-biased	No overall difference in mean body length between sexes (mean adult SVLs were similar in the two sexes), but the heads of males are significantly larger than those of females
Hikida et al. (2001)	*Plestiodon tamdaoensis*		Mixed	Males have larger heads but shorter bodies than females
Huang (1996)	*Sphenomorphus indicus*	Female-biased	None	Well-expressed SSD in SVL, where females have longer bodies than males; no significant difference in head length and head width between sexes
Ji & Du (2000)	*Sphenomorphus indicus*	Female-biased	Male-biased	Well-expressed SSD in SVL, where females have longer bodies than males; females having smaller heads than males
Terrestrial				
Bull & Pamula (1996)	*Tiliqua rugosa*	Female-biased	Male-biased	Females were significantly longer than males; males with significantly longer and broader heads than females of equivalent SVL
Griffith (1991)	*Plestiodon*	Male-biased	Male-biased	"Fasciatus" group: males are larger in SVL with relatively large heads
Hare et al. (2011)	*Oligosoma maccanni*	None	Male-biased	No statistically significant differences in body length between both sexes; sexes differ in head width
Huang (2006)	*Eutropis longicaudata*	Male-biased	Male-biased	Males have longer bodies, as well as longer, deeper, and wider heads than females
Ji et al. (2006)	*Eutropis multifasciata*	Male-biased	Male-biased	Males have longer bodies and longer heads than females; both sexes do not differ significantly in head width
Morrison et al. (2002)	*Eulamprus heatwolei*	Female-biased	Male-biased	Females obtain larger SVL and mass than males; at the same SVL males have longer, wider and deeper heads, longer hind-limbs

Table 5 Continued.

Studies	Genus/Species/ Subspecies	SSD	SShD	Body dimentions (shape and size)
Nassar et al. (2013)	*Heremites vittatus*	Female-biased	Male-biased	Females having longer bodies and males having larger heads
Olsson et al. (2002)	*Carinascincus microlepidotus*	Male-biased	Mixed	Males are slightly larger than females (in body mass and SVL); males with significantly longer heads; females with larger absolute interlimb length
Rastegar-Pouyani & Fattahi (2015)	*Heremites vittatus*	Female-biased	Female-biased	Females having longer, thicker bodies, as well as larger heads
Schwarzkopf (2005)	*Eulamprus quoyii*	None	Mixed	No significant difference between mean SVL of males and females; sexes differ in body shape; males head width, forelimb length, and mass increased more rapidly with body length than did those of females, and for a given body length, male hindlimb length was greater than that of females; females had greater trunk (interlimb) lengths
Vitt & Cooper (1985)	*Plestiodon laticeps*	Male-biased	Male-biased	Males have larger heads (total length and relative head size)
Vitt & Cooper (1986)	*Plestiodon inexpectatus*	Male-biased	Male-biased	Males have larger heads and are bigger in SVL
Vitt & Cooper (1986)	*Plestiodon fasciatus*	None	Male-biased	Males have larger head dimentions; both sexes do not differ in SVL

show pronounced size and head shape dimorphism. This is confirmed by the comparative data from the literature on other semi-fossorial species (Table 5).

Conclusion

The Snake-eyed Skink shows an evolutionary pattern by which the females are larger and possess more elongated bodies than males. This is likely related to space constraints of the eggs in the body of females and hints at fecundity selection. On the contrary, males show relatively larger heads and limbs compared to females, likely related to male–male competition. Thus, dimorphism in the Snake-eyed Skink corresponds to the "typical" two types of selection driving morphological differences between males and females. Unlike other burrowing lizards, snake-eyed skinks do show pronounced size and shape dimorphism in all subspecies, suggesting that this species is not constrained by a burrowing lifestyle, possibly due to its diminutive size.

Acknowledgements

This research received support from the SYNTHESIS Project http://www.synthesys.info/, financed by the European Community, via project *Intraspecific morphological differentiation in Ablepharus kitaibelii in relation to geographic gradients*, 2015 [HU-TAF-4883] studied specimens in Budapest, Hungary. We are grateful to Dr. Heinz Grillitsch, Dr. Silke Schweiger (NHMW, Vienna), and Dr. Judit Vörös (HNHM, Budapest) for providing access to their respective collections as well as for the support, literature, and technical equipment. We would like to thank also many colleagues for providing material and for the fieldwork assistance, as well as to Sylvia Georgieva for the assistance in the incubation of the eggs. The catching of the individuals and the incubation of the eggs was carried out under permits for scientific purposes No. 411/14.07.2011, No. 520/23.04.2013, and No. 656/08.12.2015 from the Ministry of Environment and Water, Bulgaria.

Conflict of interest

The authors declare no competing interests.

Author contributions

Conceptualization: VV, AH; Measurements: VV; Statistical analyses: AH; Main text writing and figures: VV; Editing of the text: AH. The authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Meristic and metric traits.