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Is the blue-spotted phenotype more widespread in the eastern slow worm *Anguis colchica* (Nordmann, 1840) than the western slow worm *Anguis fragilis* Linnaeus, 1758 and does it correlate with the male body size? A case study from Central Europe

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Short communication

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The blue-spotted phenotype in a slow worm can be considered as an alternative colour morph or a secondary sexual characteristic. This phenotype is known to entail an elevated predation risk; thus, its continuous presence in a population must be balanced by additional and positive fitness consequences. In this study, we show that blue-spotted males are characterised by a greater snout-vent length (SVL) than typical specimens. Importantly, the SVL of blue-spotted males reaches the magnitude of the average female size. This indicates that the presence of blue spots may involve a correlated positive effect on growth and body size. The greater body size of the blue-spotted males could enhance their survival and mating success, and thus facilitate the continued presence of a high fraction of this morph within the population. In addition, we found that the blue-spotted phenotype is more common in the eastern than the western slow worm, and the proposed fitness consequences of the blue-spotted phenotype might enhance its tendency to spread in the eastern *Anguis* lineage.

Key words: colour polymorphism, condition, divergence, sexual dimorphism.

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The maintenance of co-occurring discontinuous colour phenotypes results from an interplay of various evolutionary processes (Forsman *et al*. 2008). In general, the maintenance of such a polymorphic colouration is attributed to the opposing fitness consequences associated with each morph (Andren & Nilson 1981). In reptiles, the costs of an alternative colour phenotypes are commonly discussed in terms of alterations in the protective properties of the colouration (Madsen & Stille 1988; Wüster *et al*. 2004; Farallo & Forstner 2012). These negative consequences can be balanced by the benefits of a given colour phenotype, which can be related to improved thermoregulation (melanism; Forsman 1995) and/or sexual signalling (Ballinger & McKinney 1967; Martin & Forsman 1999; Bastiaans *et al*. 2014). Less commonly, the maintenance of a polymorphic colouration may be driven by relaxed, instead of increased, predation (Losey *et al*. 1997; Lancaster *et al*. 2014); or by non-selective factors, such as genetic drift, ancestral polymorphism or gene flow (Lawson & King1996). Clearly, the ecological significance of colour polymorphism is highly context dependent, and each example of such a polymorphism may provide a novel insight into the evolutionary processes shaping such colour variations.

A commonly observed example of polymorphic colouration occurs in European slow worms (genus *Anguis*) – a phenotype with blue spots on the dorsal and lateral side of the body is widespread within the *Anguis fragilis* Linnaeus, 1758 complex (Völkl & Alfermann 2007; Terhivuo 1990; Figure 1). However, the functions and fitness effects of this blue-spotted morph are poorly understood. As has been shown experimentally, blue-spotted slow worms are more visible to avian predators, which elevates the predation costs (Capula *et al.* 1997). In females, these costs may be balanced by positive association between the presence of blue spots and the body size (Sos 2011), which correlates with both improved survival (Civantos *et al.* 1999) and fecundity (Ferreiro & Galán 2004). On the other hand, a greater size of blue-spotted females can merely represent a side-effect of the age-related expression of the blue-spotted pattern, with no additive effects on growth (Sos 2011). The fitness benefits of this colour pattern in males are unknown, but they are conceivable given the more common occurrence of the blue-spotted phenotype in this sex (Capula *et al.* 1997; Sos 2011).

The sex-specific frequency of the blue-spotted morph might suggest that this colouration represents a secondary sexual characteristic of males, which is additionally indicated by the highest intensity of the blue-spot expression during the mating season (Capula *et al.* 1997; Sacchi *et al.* 2017). The expression of sexual characteristics in males is tightly coupled to the testosterone level (e.g. Garstka *et al.* 1991; Sinervo *et al.* 2000; Ducrest *et al.* 2008; Sacchi *et al.* 2017), while the testosterone level also impacts the animal's growth. In some species it may inhibit growth; whereas in other, even closely-related species, it enhances growth and can lead to a greater achievable body size (Cox & John-Alder 2005). Consequently, blue-spotted males can be predicted to be characterised by a larger size compared to typical non-spotted males. Such a positive effect of the blue-spotted morph on the male size could represent a potential mechanism that maintains this colour polymorphism in slow worms, due to the beneficial effects of size on male survival (Civantos *et al.* 1999), combat success and/or female choice (Capula *et al.* 1998).

Fig. 1. Unspotted (top) and blue-spotted (bottom) phenotypes of anguid lizards. Photographs by Aleksandra Kolanek.

In this study, we investigated whether this colour phenotype correlates with the male body size in a free-living slow worms. As outlined above, a greater body size can be predicted for blue-spotted males based upon at least two effects: first, the presence of blue spots could be linked to growth and eventual size through the positive impact of a high testosterone level; and alternatively, the blue-spotted pattern could be restricted to older, and therefore larger, individuals. These two scenarios may not be fully distinguishable as they lead to a similar prediction, but two additional observations can hint at which effect contributes to the male size. If the blue-spotted phenotype is associated with growth, then it should result in a body size that exceeds the size achievable by a typical male. Given that the slow worm is a species with a well-defined female-biased sexual size dimorphism (SSD), such an effect could be expected to reduce or even entirely mask the SSD. Secondly, if the presence of a blue-spotted pattern is solely age-dependent, then it might not be observable in younger (smaller) individuals. As an outcome, the range of body size variation in typical and blue-spotted males would overlap only partially. To gain an insight into whether the phenotype-size relationship and the occurrence of blue-spotted individuals are species-specific, we densely-sampled two slow worm populations, – one population of *A. fragilis* and one of *A. colchica* (Nordmann 1840) – and scanned multiple populations of both species for the presence of the blue-spotted phenotype.

We collected data on 13 populations of *A. colchica* and 18 populations of *A. fragilis* (Fig. 2, Table 1). Two of the populations, *A. colchica* from the San River Valley and *A. fragilis* from Górażdże, were densely sampled (n=104 and n=115, respectively); whereas the samples from other populations were

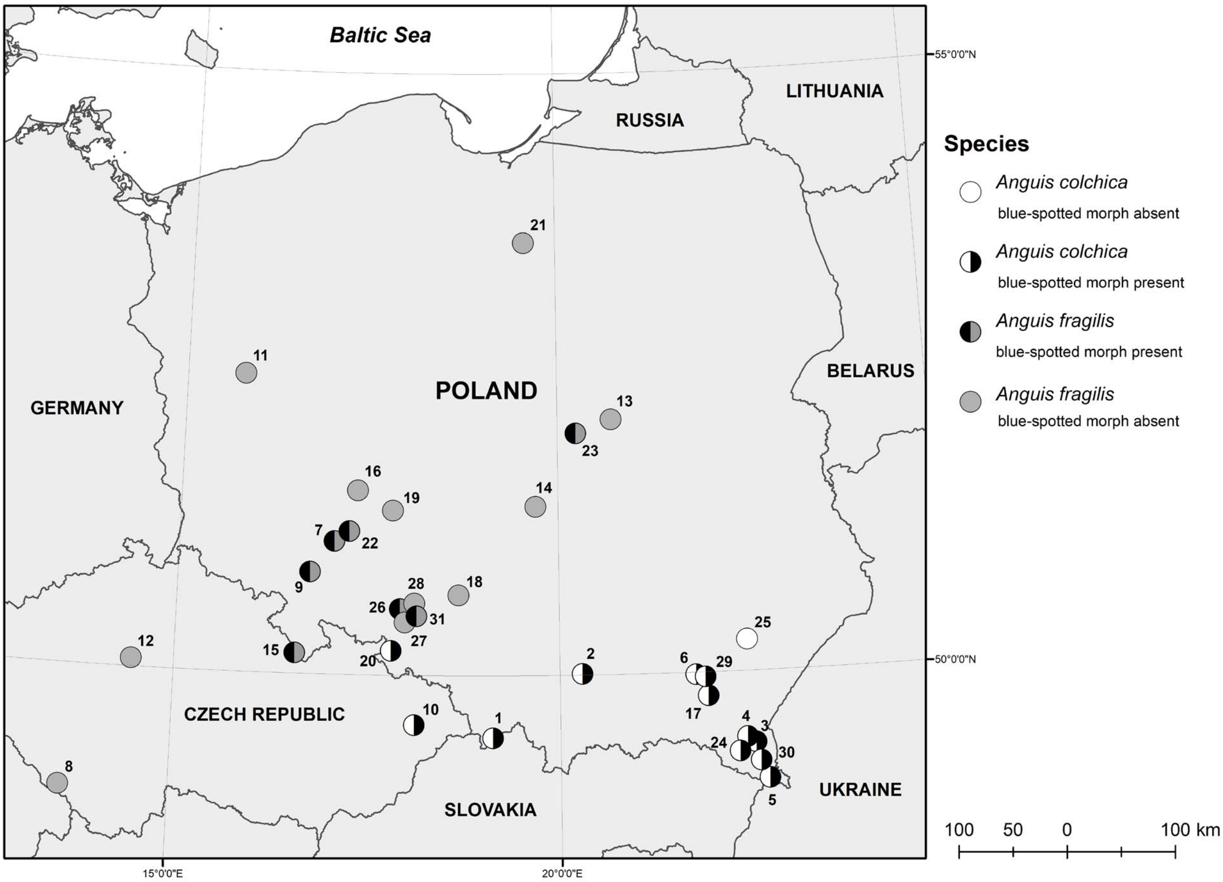

Fig. 2. Map of the localities of the populations sampled in this study. *Anguis colchica* populations: 1 – Beskid Żywiecki, 2 – Kłaj, 3 – Bóbrka, 4 – Myczkowce, 5 – Ustrzyki Górne, 6 – Czudec, 10 – Štramberk, 17 – Lutcza, 20 – Kuźnia Raciborska, 24 – Baligród, 25 – Leżajsk, 29 – Lutoryż, 30 – San River Valley; *Anguis fragilis* populations: 7 – Wrocław, 8 – Šumava, 9 – Sulistrowiczki, 11 – Pszczew, 12 – Prague, 13 – Podkowa Leśna, 14 – Piotrków Trybunalski, 15 – Niemojów, 16 – Milicz, 18 – Lubliniec, 19 – Ligota, 21 – Iława, 22 – Byków, 23 – Bartniki, 26 – Leśniczówka, 27 – Dzioły, 28 – Susły, 31 – Górażdże.

smaller (from 3 to 16 specimens; see Table 1). Most of the data for the San River Valley population was extracted from a published source (Błażuk 2007) and supplemented by our original measurements from the same locality collected in the years 2008-2020, while morphometric data on *A. fragilis* from Górażdże was collected by us during the years 2015-2018. Data on 12 additional populations of *A. colchica* and 17 populations of *A. fragilis* was gathered mostly in 2014-2017 during earlier studies (Bury *et al.* 2020), as well as from museum collections (Fig. 2, Table 1). The museum collections used in the study are listed below.

Anguis colchica:

San River Valley population: Museum of Natural History of the University of Wrocław MNHW-Reptilia-0247 (5 specimens);

Štramberk population: National Museum in Prague (NMP6V) 7415-1-3, 70591, 72822, 74103-1,2, 74119-1,2, 74121-1,2, 74132, 74132-1,2, 74153.

Anguis fragilis:

Prague population: NMP6V 32388, 35089/3, 74407, 74543, 74990, 75517;

Šumava population: NMP6V 31747, 32640, 34275, 35100.

In the case of the San River Valley and Górażdże populations, the slow worms, except newborns and yearlings, were collected throughout the active season from spring to autumn. For each specimen, the snout-vent length (SVL), sex, tail condition (intact or broken) and colour phenotype (blue-spotted or typical) were assessed. Because the brightness of the blue spots can depend on the shedding cycle and season, we encoded this variable as a categorical one [presence/absence of spots] instead of a continuous one. Body mass was excluded from the dataset, because it can vary considerably, e.g. in relation to the absorptive state, and therefore it cannot be reliably standardised under field conditions.

For the additional sites, the number of sampled specimens per population was lower than the num-

Table 1

List of the sampled populations of the eastern slow worm (*Anguis colchica*) and the western slow worm (*Anguis fragilis*). N – number of specimens from the sampled population. ‘Blue-spotted’ refers to the presence (+) or absence (–) of the blue-spotted phenotype in the sample; ‘Site ID’ is the number of the population in Figure 2.

Population	N	Geographic coordinates		Blue-spotted	Site ID
		Latitude (N)	Longitude (E)		
Anguis colchica					
Beskid Żywiecki	4	49°48′	19°14′	+	1
Kłaj	13	50°01′	20°29′	+	2
Bóbrka	6	49°42′	22°44′	+	3
Myczkowce	12	49°44′	22°41′	+	4
Ustrzyki Górne	5	49°10′	22°65′	+	5
Czudec	15	49°97′	21°80′	+	6
Štramberk	15	49°59′	18°12′	+	10
Lutcza	8	49°80′	21°91′	+	17
Kuźnia Raciborska	6	50°20′	17°81′	+	20
Baligród	3	49°33′	22°28′	+	24
Leżajsk	4	50°26′	22°43′	–	25
Lutoryż	10	49°96′	21°88′	+	29
San River Valley	104	49°25′	22°55′	+	30
Anguis fragilis					
Wrocław	5	51°10′	17°04′	+	7
Šumava	4	48°98′	13°62′	–	8
Sulistrowiczki	6	50°84′	16°,73′	+	9
Pszczew	6	52°47′	15°78′	–	11
Prague	6	50°06′	14°45′	–	12
Podkowa Leśna	3	52°12′	20°73′	–	13
Piotrków Trybunalski	3	51°40′	19°70′	–	14
Niemojów	7	50°17′	16°56′	+	15
Milicz	6	51°53′	17°34′	–	16
Lubliniec	5	50°66′	18°68′	–	18
Ligota	5	51°36′	17°,81′	–	19
Iława	3	53°59′	19°56′	–	21
Byków	4	51°19′	17°24′	+	22
Bartniki	5	52°01′	20°25′	+	23
Leśniczówka	9	50°52′	18°01′	+	26
Dzioły	16	50°51′	18°03′	–	27
Susły	6	50°53′	18°06′	–	28
Górażdże	115	50°52′	18°04′	+	31

bers in the San River Valley and Górażdże, but was comparable among both species (mean: 8.42 for *A. colchica* and 5.82 for *A. fragilis*, t=1.87, p=0.07). We did not include these specimens in the morphometric analysis due to their low number and a potentially high interpopulation variability. Moreover, morphometric measurements were not gathered for all of the specimens from these populations.

Data on the SVL was analysed using the General Mixed Model that compared three groups: typical males (N=29), blue-spotted males (N=27) and typical females (N=48). Only one blue-spotted female was found in the analysed population of *A. colchica*, which precluded it from a formal analysis and it was not included in the final dataset. Given that the measurements of *A. colchica* originated from two sources (Błażuk 2007 and our survey), we included the source of the data as a random factor in the model, but it appeared to be non-significant (p=0.26). We analysed the morphometric data only for the *A. colchica* population, because the number of blue-spotted individuals in *A. fragilis* appeared to be too low for a statistical comparison (see below). The normality of the SVL data distribution was assessed prior to the analysis and no data transformation turned out to be necessary. The occurrence of the blue-spotted phenotype in both species (all populations) was analysed by comparing the number of populations for which the blue-spotted phenotype was or was not recorded with a 4x4 Chi^2 test. In addition, we analysed the tail loss frequency in the slow worms (all populations). We compared the frequency of tail loss in the blues-spotted vs typical males of *A. colchica,* as well as the whole-population frequency of tail loss between *A. fragilis* and *A. colchica* with a 4x4 Chi^2 test. All analyses were conducted using the Statistica software (ver. 13.3, StatSoft Poland).

We found that the SVL differed significantly among the tested groups (females, typical males and blue-spotted males) ($F_{2,100}$=9.33; p=0.002). A post-hoc test revealed that the typical males were significantly smaller than the females (p<0.001) and blue-spotted males (p=0.015), but there were no detectable differences between the blue-spotted males and the females (p=0.613). Furthermore, the range of the body size variation overlapped largely between the blue-spotted and typical males (Figure 3). Although it was not possible to test the effects of the colour phenotype on the SVL in *A. fragilis* due to an extremely low number of blue-spotted individuals (N=1), we found a clear difference in the frequency of the blue-spotted phenotype in the *A. colchica* vs *A. fragilis* populations. Specifically, the share of this phenotype reached 26% in *A. colchica* (27 blue-spotted per 104 individuals), while it only reached less than 1% in *A. fragilis* (1 blue-spotted per 115 individuals) (Chi^2=30.84, df=1, p<0.001). We further observed that, at the multi-population level, the blue-spotted phenotype occurs more commonly in *A. colchica* (12 per 13 populations) than in *A. fragilis* (6 per 18 populations) (Chi^2=10.78; df=1, p=0.001). Finally, the frequency of tail loss in the blue-spotted males did not differ significantly from the typical morph (Chi^2=0.22; df=1, p=0.643), but the whole-population frequency of tail loss was higher in *A. colchica* than in *A. fragilis* (Chi^2=8.54; df=1, p=0.004).

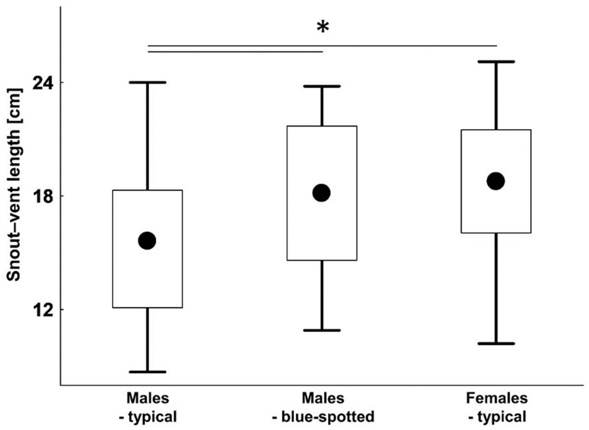

Fig. 3. Body size of normally-coloured males, blue-spotted males and typical females of *Anguis colchica*. Lines with an asterisk indicate differences that are significant (p<0.05). Box – 25-75%; whiskers – non-outlier range (1.5 of the interquartile range below the first quartile or above the third quartile); black circle – mean.

Our study is the first to show the association between the blue-spotted phenotype in eastern slow worms and the male body size – as expected, the blue-spotted males appeared on average to be larger than typical males. The data we were able to obtain did not allow us to exclude or corroborate the contribution of the ontogenetic colour change to the observed pattern, but it is probable that at individual's age at least partially explains the larger size of blue-spotted males. However, in our study the ranges of body size variation in both of the phenotypes in males largely overlapped, meaning that both fully grown and older individuals are present among the males without spots. Furthermore, blue-spotted males appeared to be not only larger than typical males, but also to exceed the size of typical males to a level comparable to the female size (Figure 3). It is therefore conceivable that additional non-age-related factors contribute to the greater SVL of the blue-spotted males. The blue colouration in lizards often results from a high concentration of steroid hormones (Garstka *et al.* 1991; Ducrest *et al.* 2008), including testosterone in the case of males. Experimental injections with testosterone have even been shown to enhance the expression of the bluish colouration, while at the same time, the testosterone may accelerate growth (Uller *et al.* 2007; Cox *et al.* 2008). To fully resolve what mechanisms underlie the observed association between colour phenotype and male body size, further studies that are designed to assess the growth rates, individual's age and testosterone levels in different colour morphs are necessary.

The high frequency of the blue-spotted phenotype in *A. colchica* can be maintained due to the positive fitness consequences attributed to the role of the body size and colouration in male mating success. Specifically, the male body size in slow worms is positively associated with the likelihood of winning combats during the mating period (Capula *et al.* 1998). Therefore, larger-bodied blue-spotted males could be more likely to attain higher combat success and more chances for copulation. In addition, a conspicuous male colouration is known to attract females in many lizard species (e.g. Baird *et al.* 1997; Hamilton & Sullivan 2005); thus, one cannot exclude the positive role of blue spots on the choice of mate in the slow worm. We suggested that similar mechanisms underlie the maintenance of the blue-spotted phenotype in females. For example, a larger body size in females with the blue-spotted phenotype could also be related to reproductive success, i.e. by the additive effect of an increased size on fecundity (Ferreiro & Galán 2004).

Finally, we observed a clear species-specific variation in the multi-population scale occurrence and the within-population frequency of the blue-spotted phenotype (Figure 2), with both being higher in *A. colchica* compared to *A. fragilis*. Such a spread of the blue-spotted phenotype in the eastern slow worm could have been driven by the relaxed costs or enhanced benefits of this phenotype. Our data on the tail loss frequency as an indicator of the costs related to the predation pressure was inconsistent. A comparable share of males with broken vs intact tails within both phenotypes suggests that the blue-spotted slow worms do not suffer a higher predation risk, contrary to previous reports (Capula *et al.* 1997). On the other hand, the whole-population tail loss frequency was found to be higher in the population of *A. colchica* compared to that of *A. fragilis*. Nonetheless, the tail loss frequency is not an accurate measure of the predation pressure (Jaksić & Greene 1984), so a further and more precise assessment of the predation risks in eastern and western slow worm clades is necessary. Instead of relaxed predation, we suggest that the above discussed benefits of the blue-spotted phenotype associated with reproductive success could contribute to the more common occurrence of the blue-spotted morph in the eastern slow worm. This could indicate an asymmetric sexual selection among both species, which in turn could accelerate the divergence of the slow worm clades (Benkovský *et al.* 2021).

Author Contributions

Research concept and design: S.B., B.B.; Collection and/or assembly of data: S.B., A,K., G.S., K.K., B.Z., B.N., B.B.; Data analysis and interpretation: S.B., B.B.; Writing the article: S.B., B.B.; Critical revision of the article: S.B., A,K., G.S., K.K., B.Z., B.N., B.B.; Final approval of article: S.B., A,K., G.S., K.K., B.Z., B.N., B.B.

Conflict of Interest

The authors declare no conflict of interest.

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