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Is It Function or Fashion? An Integrative Analysis of Morphology, Performance, and Metabolism in a Colour Polymorphic Lizard

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Abstract: Colour polymorphism may be accompanied by alternative expressions of phenotypic traits that are directly or indirectly related to fitness, and selection forces may act on the traits separately or concurrently. In polymorphic species, natural selection may act through frequency- or density-dependent mechanisms and maintain polymorphism through interactions among morphs. We used an integrative approach to examine functionally relevant and interrelated life history traits in the context of colour polymorphism in the European wall lizard (*Podarcis muralis*). Body, head and limb morphology, bite and locomotor performance, and physiology, particularly metabolic and antioxidant capacity, were analysed in the three pure colour morphs (yellow, orange, white) and the two mosaic morphs (yellow-orange and white-orange). Morphological differences between morphs were present but subtle and consisted mainly of variations in head length. Head size and bite force were strongly associated between and within morphs. Limb and boot morphology and locomotor performance (sprinting and climbing) were variably associated among morphs. Finally, variation in biochemical indicators of cellular metabolism and antioxidant capacity appeared to be largely independent of morphology and performance. The results provide evidence for existing and non-existing relationships between colour and morphology, performance, and physiology that could have short- and long-term effects on selection.

Keywords: Lacertidae; colour morphs; sprint speed; climbing; bite force; physiology

1. Introduction

Colour is one of the most variable and noticeable phenotypic traits in the natural world. In non-avian reptiles, including lizards, pigments and structures responsible for colour production are contained in specialized cells known as dermal chromatophores [1–3]. The variation in chromatophore content and the combination between the different chromatophore types generates the high variability of colours and patterns described in this animal group. In correspondence, diurnal lizards possess a complex colour vision system composed by four different cone types, as well as double cones, allowing the discrimination of a large range of colours [4]. Most colour patches of lizards are often interpreted as visual signals, especially those showing a conspicuous appearance to conspecifics (e.g., [5–8]). Researchers often study the putative signalling function of these conspicuous patches exploring the relationship between some colour properties and variables related to individual quality. However, fewer studies have examined the relationship between colour traits and direct indicators of individual fitness and quality, such as physiology and performance.

Studies on lizard coloration frequently recover biologically relevant differences among individuals correlated with colour variation, either depending on ontogeny e.g., [9], reproductive status e.g., [10], performance e.g., [11–13] or body condition that can be affected, for example by parasite load, disease and immune system function e.g., [14,15] and stress level e.g., [16]. Specifically, the content of carotenoids within the xanthophores may arise from the physiological trade-off between carotenoid-based coloration and immune and antioxidant functions [3]. Similarly, colours produced by structural elements involved in colour production may be affected by various stressors, by testosterone-dependent melanin deposition, or a combination of both (e.g., [5,6]).

On the other hand, differences in an organism's morphology may result in differences in performance which in turn translate into variation in fitness [17–19]. This link between morphology, performance and fitness is usually addressed in the framework of the ecomorphological paradigm [17]. Morphological traits represent a considerable part of the phenotype, and it is through these structures that organisms interact with their environment [20]. Natural and sexual selection will act on morphology to optimize whole-organism performance by influencing the traits involved in their daily activities—basic ecological functions (e.g., feeding, escape from predators, habitat, and refuge use) and social interactions (e.g., intraspecific antagonistic behaviour, territory and mate acquisition, competition with conspecifics). However, morphology-performance relationships are intricate, and they are modulated by behaviour and physiology. The two most studied animal functional systems are locomotor performance along with its associated morphology (e.g., limb length) and bite performance along with its associated head morphology. Both systems are central in many basic activities and they might be subject to strong selective influences e.g., [21–27].

In individuals' life, mostly physiological performance (metabolism) directly contributes to growth, the immune system, and the abilities to perform and behave in a way to achieve survival and reproductive success. The mitochondrial respiratory chain is the key process of an organism's basal metabolism at the cellular level [28]. On the biochemical level, metabolism is constrained by enzyme activities together with mitochondrial oxidative capacities that reflect the maximal rate at which metabolic processes can occur [29]. Potential metabolic activity (PMA) is a direct enzymatic parameter that depends on the concentration [30] and characteristics [31] of enzymes, and it has previously proved to be a useful measure for assessing metabolic variation in lizards e.g., [32,33]. Thus, PMA can provide crucial information about the physiological properties of an organism's fundamental niche e.g., [34].

Metabolic activity produces reactive oxygen species (ROS) that must be eliminated with corresponding antioxidative mechanisms to avoid oxidative damage. Oxidative stress is an imbalance between ROS production and antioxidant defences, resulting in oxidative damage [35,36]. If the rate of ROS production is higher than the capacity of antioxidant systems, ROS can cause cellular damage [37]. Important parameters in this context are the metabolic rate potentially affecting the production of ROS, the degree of oxidative damage, and antioxidant defence mechanisms [33,36]. A good proxy of antioxidative capacity is the catalase activity (CAT). Catalase is an enzyme with the principal function of transforming oxygen peroxide (ROS) into water and oxygen [38]. PMA and CAT have been found to correlate with various life history traits. For example, with seasonal variation [39,40], contrasting environments [41], habitat conditions [42], species competitive ability [43], or high-altitude adaptation [33]. Therefore, metabolic and antioxidant capacity is expected to be a general life-history characteristic and thus connected with behavioural and performance abilities, which all have to some extent been correlated with coloration.

Colour polymorphisms involving genetically determined discrete colour morphs are excellent models to test many of the hypotheses on the underlying causes of selection. Although many polymorphisms are often considered to be mostly driven by sexual selection [44], the evolutionary maintenance of polymorphic systems is inevitably affected by different selective pressures. In the Common Wall lizard (*Podarcis muralis*), a polymorphic species with different ventral colours in both males and females, preliminary evidence suggests the polymorphism evolves under a complex interaction between sexual and natural selection [7,45,46]. In this species, white, yellow and orange pure morphs, as well as white-orange and yellow-orange mosaic morphs, may coexist in the same population [47–49]. Yellow and/or orange coloration is often expressed in both throat and belly in males, but, depending on the population, females only show these colors in their throat [48]. Although colors describing morphs are only expressed ventrally, this coloration is visible to conspecifics laterally and its exhibition is modulated behaviorally (subtly displayed when the lizard raises the head, equally done by all morphs) and is dependent of thermoregulation [49]. Colour morphs of *P. muralis* (see Figure A1) are genetically determined [50] and fixed at maturity in both sexes, although local morph frequencies often differ between sexes [45,48]. Colour may cover the whole ventral surface of the lizard, but it is usually first expressed on the throat during the growth, which is used to assign the colour morph since there is correspondence between visual identification and spectral data [48]. Pterin and carotenoid pigments are involved in the production of yellow and orange colours in this species, and just recently their molecular and cellular bases have become resolved. Genomes of sympatric colour morphs of *P. muralis* are virtually undifferentiated, except for two small regulatory regions near genes associated with pterin and carotenoid metabolism [50]. Carotenoid and pterin compounds are known to be involved in a wide range of vital metabolic processes [51,52]; thus, we might expect that variation in colour expression (i.e., morphs) will be related to the metabolic capacity level.

Despite this rather extensive knowledge of the life history traits, behaviour, and physiology of colour morphs in *P. muralis* (see references above and in the Discussion), there is a major gap regarding the link between coloration, morphology, and physiology, namely whether colour polymorphism translates into variation in physiology-metabolism, since metabolism is central to energy balance, while oxidative stress is central to lifespan and ageing or stress resistance. In this study, we took an integrative approach to examine several functionally relevant and interrelated traits-morphology, performance, and metabolism-in the context of colour polymorphism. We hypothesise that alternative colour morphs may express (different) associations between performance and morphology [24]. Associations between metabolic and antioxidant capacity and performance are poorly understood, but are to be expected given the direct relationship between muscle activity and metabolic rate [28]. We also predict performance differences between morphs (running speed and bite force) according to variation in locomotion behaviour [53]. By including mosaic morphs in our analysis, which are less abundant in the field [45,46], we can also test whether trait expression is mixed between the two corresponding morphs or whether they may be negatively selected. An alternative hypothesis is that other mechanisms, such as multivariate selection (e.g., hybridization), may balance and mask variation between colour morphs. Overall, the results will help clarify whether alternative associations between morphology performance and metabolic performance are related to population-level polymorphism. Such results could lead to a better understanding of the mechanisms involved in the maintenance or the release of alternative morphs within populations.

2. Materials and Methods

2.1. Sampling

All individuals were collected in Llívia, in Cerdanya plateau (eastern Pyrenees, 42°27′33.6″ N 1°58′53.3″ E), where *P. muralis* is abundant and widely distributed across different habitats: rocks, vegetation, bare ground, and human buildings. The study was conducted during June 2019, within the breeding season. To minimize any effects of ontogeny and sex on colour expression, all individuals considered were adult males with snout vent-length $\geq$ 56 mm (i.e., with a fully developed ventral coloration; [48]). A previous study using spectrophotometry and visual modelling verified that colour morphs are discriminable by lizards in the same way that the human eye can do [54]. Thus, ventral colouration was inspected by eye and each individual was assigned to three colour morphs (white, orange and red) or two mixed colour morphs (white-orange or white-red) (Figure A1). We collected a total of 94 adult individuals (white = 24, orange = 24, yellow = 26, white-orange = 9, yellow-orange = 11) by noosing [55]. Lizards were placed in cloth bags and transported to the laboratory. All lizards used in experiments had intact limbs, fingers/toes and fully grown tails (original or fully regenerated). They were housed in individual terraria where they were fed with live mealworms and provided water ad lib. Lizards were kept in captivity for a total of five days and released back to the site where they had been captured. Collecting permit SF/0092/2019 was provided by Direcció General de Polítiques Ambientals i Medi Natural, Generalitat de Catalunya. This study was approved by the ethical guidelines of University of Porto.

2.2. Morphological Variables

In all individuals captured, we measured, using electronic calipers (precision 0.01 mm), the following linear biometric traits: snout-vent length (SVL), trunk length (TRL), pileus length (PL), head length (HL), head width (HW), head height (HH), mouth opening (MO), fore limb length (FLL) and hind limb length (HLL) (see [56] for a detailed description of variables). All morphological traits were log-transformed prior to data analyses to ensure normality in the distribution. Head size (HS) was calculated as a geometric mean of HL, HW and HH, which in the logarithmic form becomes the arithmetic mean of log-transformed head dimensions [24].

2.3. Performance Traits

All experiments to quantify functional performance were carried out at a room temperature around 31 °C, which is approximately the selected body temperature of the species in summer [57]. All lizards were placed for at least 1 h in a terrarium exposed to an infrared lamp of 150 W, prior to and in between trials, allowing them to thermoregulate and achieve their preferred body temperatures [58].

Three types of locomotor performance were measured [24]: sprint speed (SPRINT), climbing capacity (CLIMB), and manoeuvrability (MANO). Sprint speed on a horizontal surface was measured by chasing animals along a 1-m-long cork substrate [20,59,60]. Climbing performance was obtained by chasing animals up a similar racetrack, tilted to an angle of 60°. Cork was used as a substrate because it provides very good traction [61]. To measure manoeuvrability, a 0.5-m long and 15-cm-wide pinboard was used. This pinboard was made of 8-mm diameter pins placed at equal distances of 35 mm [20,25]. Animals were allowed to recover between trials (for approx. 2 h), and for each type of locomotor performance three trials were made. All locomotor trials were recorded with a digital camera (Olympus Tough tg-5) at a filming speed of 60 frames per second. The position of the lizard across each trial was digitized using Tracker—video analysis and modelling tool software (v5.1.5, [62]). The highest instantaneous speed [63] recorded across three trials was taken as maximum performing capacity in each of the three types of racetrack and log-transformed for further analyses.

After the locomotor tests, bite force was measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland). Bite force was measured by motivating the lizard to bite a pair of thin metal plates connected to the force transducer (see [20] for a detailed description). Each lizard was tested five times to ensure that the maximal individual bite force per individual was obtained. The maximum bite force measure per individual was log-transformed for further analyses.

2.4. Potential Metabolic Activity (PMA) and Catalase Activity (CAT)

We estimated PMA by the iodonitrotetrazolium chloride (INT) reduction capacity and the antioxidative capacity by catalase activity (CAT). The assay of PMA was adopted by [30] and modified by [64]. The INT reduction method is used as a proxy for cellular respiration [32,43] while taking into account that the reduction of INT can also be extramitochondrial and associated with cytosolic, lysosomal and peroxisomal fractions [65,66]. The antioxidative capacity by catalase activity (CAT) serves as a proxy of antioxidant enzyme activity (capacity). For the biochemical analysis of both PMA and CAT, we used tail tips, whose removal has already demonstrated to produce a minimal behavioural disturbance on wall lizards [67]. We placed individual tail tips in 2 mL Eppendorf vials and immediately dropped them in the liquid nitrogen storage bottle. Samples were transported on dry ice and stored at −80 °C until analysis. We homogenized each tail tip with liquid nitrogen in a mortar and pestle to obtain finely ground powder. The grounded tissue was weighted to determine the wet mass and used for the homogenate preparation. We added to the grinded tissue 3 mL ice-cold homogenization buffer (0.1 M sodium phosphate buffer pH = 8.4; 75 µM $MgSO_4$; 0.15% (*w*/*v*) polyvinyl pyrrolidone; 0.2% (*v*/*v*) Triton-X-100) and sonicated for 20 s. Samples were then centrifuged for 4 min at 0 °C at 10,000 rpm. First, PMA analysis was proceeded and the other half of the homogenate for CAT analysis was stored at −80 °C until analysis.

For estimation of PMA, two replicates of 30 µL samples and one blank without the homogenate were all incubated at three different temperatures: 26 °C, 31 °C and 36 °C for 30 min with a 150 µL substrate solution (0.1 M sodium phosphate buffer pH = 8.4; 1.7 mM NADH; 0.25 mM NADPH; 0.2% (*v*/*v*) Triton-X-100) and 50 µL reagent solution (2.5 mM 2-(p-iodophenyl)-3-(nitrophenyl)-5-phenyl tetrazolium chloride (INT) solution). The reaction was stopped by adding 50 µL of stopping solution (formalin: concentrated H_3PO_4; 1:1 *v/v*). Aliquots of 30 µL homogenate was added into blanks. Formazan production was determined spectrophotometrically from the absorbance of the sample at 490 nm using a microplate reader (Synergy MX BioTek, BioTek, Winooski, VT, USA). The values of PMA were estimated as the INT reduction capacity ($\mu L\ O_2\ mg^{-1}$ protein h^{-1}) as:

$$\text{INT reduction capacity} = (\text{Abs } 490 \text{ nm} \times \text{Vr} \times \text{Vh} \times 60 \times 1.30)/(\text{Va} \times \text{S} \times \text{t} \times 1.42),$$

where Abs 490 nm is the absorption of the sample; Vr is the final volume of the reaction mixture (mL); Vh is the volume of the original homogenate (mL); Va is the volume of the aliquot of the homogenate; S is the protein mass of sample (mg); t is the incubation time (min); 1.30 is the factor for path length correction [68] and 1.42 is the factor for conversion to volume O_2 [69].

CAT activity was determined according to [38]. We mixed 0.3 mL of the homogenate with 1.7 mL of 50 mM potassium phosphate buffer pH 7.0. We added 1 mL of 30 mM hydrogen peroxide, prepared in 50 mM potassium phosphate buffer pH 7.0, to give a concentration of hydrogen peroxide of 10 mM. Decomposition of the hydrogen peroxide was followed spectrophotometrically by reading absorbance every 30 s at 240 nm for 3 min at 25 °C using quartz cuvettes with a path length of 10 mm and a Lambda UV/V is spectrophotometer (PerkinElmer, Waltham, MA, USA). We expressed enzyme activities in enzyme units (U), where one U being the amount of CAT that degrades one µmol of hydrogen peroxide in 1 min ($\varepsilon 240 = 43.6\ M^{-1}\ cm^{-1}$). We divided these results by the total amount of protein to give the specific CAT activity per mg protein.

We determined protein concentration of the homogenate with a Pierce™ BCA Protein Assay Kit (Thermo Scientific, Waltham, MA, USA) using a microplate reader by following the manufacturer's instructions.

2.5. Statistical Analyses

To investigate if there were differences in body (SVL) and head size (HS) between morphs, we used ANOVA comparisons. Next, ANCOVA models were run using each measured morphological trait as the response variable and morph as a predictor, and we also used SVL or HS as a covariate depending on the examined morphological trait. We also performed ANCOVA comparisons on each type of locomotor speed, bite force performance and physiology trait separately with the same design and considering SVL—in the case of locomotor performance and physiology—and HS—in the case of bite force—as covariates. Throughout, we always used permutation-based ANOVA procedures using 1000 randomizations as implemented in the RRPP R-package [70]. Subsequently, we performed posthoc comparisons (Tukey's HSD) to test for differences between pairs of morphs of significant effects.

To investigate the multivariate association between two blocks of traits, we used two-block partial least squares regression (PLS) as implemented in the plsr function of the pls R-package [71]. We specifically investigated the associations: (i) between each performance trait and associated morphology traits and (ii) between each physiology trait and associated performance and morphology traits. One block included a single trait and, the other block included multiple traits of morphology or performance (see Table A1 for details on the traits used in each block). We performed this analysis for all the morphs together and for each morph separately. All statistical analyses were performed using R v. 4.0.3 [72].

3. Results

3.1. Morphology

Captured males of three pure colour morphs and two mosaic colour morphs did not differ in body and head size (SVL and HS) or limb length (FLL and HLL) (Tables 1 and 2). ANCOVA comparisons with SVL as a covariate indicated that TRL scaled allometrically with SVL, following different allometric slopes in different morphs (Table 2, Figure 1). ANCOVA comparisons with HS as covariate exhibited a significant difference between morphs in HL and only a marginal significant effect when considering HW (Table 2, Figure 2). The only significant pairwise comparison between morphs was the one between HW of the yellow-orange and the white morph ($p = 0.034$, Figure 2), while the difference in HW approached significance between the yellow-orange and orange morph ($p = 0.06$, Figure 2). No other pairwise comparison between morphs in HW and HL were significant (post-Hoc results all $p > 0.05$).

Table 1. Mean values (Mean) with standard deviations (SD) for all studied traits (morphology, performance and metabolic) classified by colour morphs of *Podarcis muralis*. W-O and Y-O indicate the white-orange and yellow-orange intermediate morphs respectively. See Materials and Methods for variable abbreviations.

		Orange N = 22	**White** N = 22	**Yellow** N = 24	**W-O** N = 8	**Y-O** N = 10
SVL	Mean	68.59	68.58	67.09	66.91	66.72
(mm)	+/−SD	3.57	2.86	3.97	2.96	3.29
TRL	Mean	32.47	32.66	31.58	32.65	32.10
(mm)	+/−SD	2.71	1.75	1.59	1.54	2.62
HL	Mean	25.86	25.50	24.59	25.20	25.00
(mm)	+/−SD	1.51	1.36	1.75	1.46	1.41
PL	Mean	16.62	16.44	16.40	16.08	16.25
(mm)	+/−SD	0.81	0.91	1.05	0.64	0.76
HH	Mean	8.97	8.95	8.89	8.71	8.79
(mm)	+/−SD	0.45	0.58	0.61	0.30	0.54
HW	Mean	6.87	6.78	6.73	6.69	7.12
(mm)	+/−SD	0.58	0.66	0.50	0.45	0.56
FLL	Mean	21.83	20.93	21.38	21.40	21.72
(mm)	+/−SD	1.22	1.54	1.29	1.21	1.02
HLL	Mean	34.77	34.00	33.41	33.70	34.38
(mm)	+/−SD	1.55	1.63	2.41	2.39	2.09

Table 1. *Cont.*

		Orange **N = 22**	**White** **N = 22**	**Yellow** **N = 24**	**W-O** **N = 8**	**Y-O** **N = 10**
SPRINT	Mean	195.84	192.62	185.43	195.07	192.59
(cm/s)	+/−SD	27.81	24.67	22.46	15.30	29.61
CLIMB	Mean	147.05	137.93	141.86	142.58	127.52
(cm/s)	+/−SD	22.32	20.87	14.47	19.32	30.55
MANO	Mean	99.54	100.08	104.00	98.76	104.07
(cm/s)	+/−SD	11.93	9.09	17.84	10.20	15.74
BITE	Mean	5.98	5.95	5.88	6.01	5.95
(N)	+/−SD	1.10	1.04	1.35	1.21	1.32
PMA26	Mean	27.77	24.99	27.01	21.89	26.89
(μLO$_2$/mg pr/h)	+/−SD	11.68	7.37	9.03	5.71	10.99
PMA31	Mean	39.86	34.17	39.08	29.76	34.56
(μLO$_2$/mg pr/h)	+/−SD	13.85	11.31	12.94	10.60	14.95
PMA36	Mean	44.11	36.27	43.82	35.49	34.95
(μLO$_2$/mg pr/h)	+/−SD	17.2	11.03	14.64	14.79	17.53
CAT	Mean	5.95	5.09	5.32	4.40	5.43
(U/mg pr)	+/−SD	2.34	2.05	2.05	1.85	3.07

Table 2. Results of AN(C)OVA comparisons on morphology, body part dimensions in relation to SVL; head dimensions relative to head size (HS); physiology (potential metabolic capacity; PMA) at three temperature regimes and catalase activity (CAT) traits relative to SVL, and performance considering the effect of colour morph (morph) and the interaction with body size (SVL, in the case of locomotion traits) or head size (HS, in the case of BITE) as a covariate (represented by X). df: degrees of freedom, F: F-statistic, *p*: corresponding *p*-value. Significant effects are marked in bold. See Materials and Methods for variable abbreviations.

		SVL		**HS**	
	df	**F**	***p***	**F**	***p***
morph	4	1.36	0.232	0.654	0.592
Residuals	88				
Total	92				

		TRL		**FLL**		**HLL**	
	df	**F**	***p***	**F**	***p***	**F**	***p***
log(SVL)	1	83.56	**0.001**	28.31	**0.001**	43.34	**0.001**
morph	4	0.85	0.506	2.03	0.095	1.45	0.233
log(SVL):morph	4	3.81	**0.009**	0.88	0.483	0.60	0.654
Residuals	83						
Total	92						

		HL		**PL**		**HW**		**HH**		**MO**	
	df	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***
HS	1	145.89	**0.001**	170.87	**0.001**	200.57	**0.001**	242.74	**0.001**	76.08	**0.001**
morph	4	2.80	**0.029**	1.12	0.362	2.44	0.058	2.06	0.084	0.67	0.630
HS:morph	4	0.62	0.627	0.08	0.982	1.04	0.400	0.45	0.777	1.00	0.388
Residuals	83										
Total	92										

		PMA26		**PMA31**		**PMA36**		**CAT**	
	df	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***
log(SVL)	1	0.51	0.519	0.18	0.670	0.21	0.670	0.79	0.383
morph	4	0.42	0.788	1.45	0.239	1.83	0.141	0.81	0.515
log(SVL):morph	4	1.03	0.398	0.26	0.892	1.20	0.320	0.23	0.931
Residuals	76								
Total	85								

Table 2. *Cont.*

		BITE		SPRINT		CLIMB		MANO	
	df	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***
log(X)	1	131.21	**0.001**	2.31	0.132	3.50	0.062	0.11	0.746
morph	4	0.84	0.507	0.73	0.560	1.39	0.232	0.51	0.735
log(X):morph	4	2.27	0.075	0.71	0.589	2.08	0.115	0.74	0.557
Residuals	83								
Total	92								

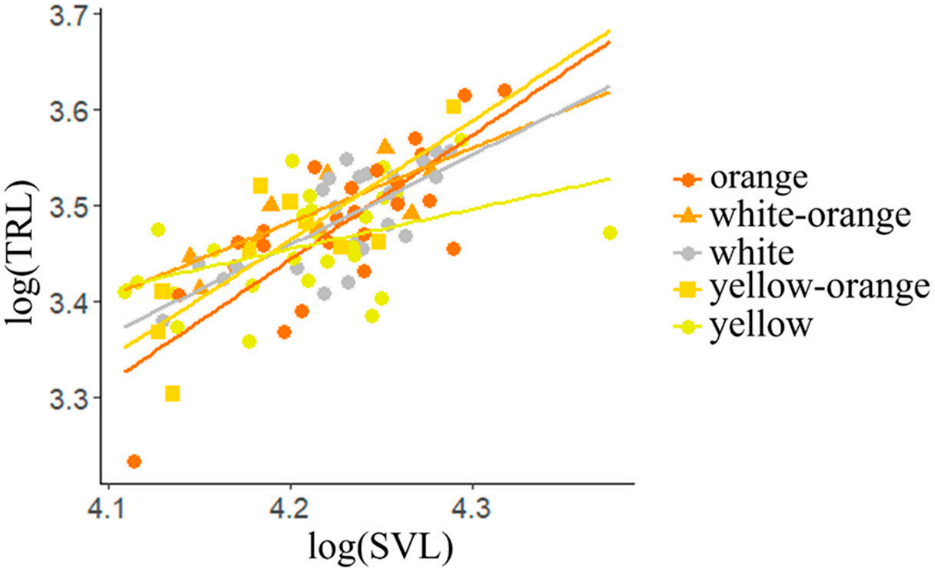

Figure 1. Relationship of trunk length (TRL) with snout–vent length (SVL) in the different morphs.

3.2. Performance Traits

ANCOVA comparisons using SVL (SPRINT, CLIMB and MANO) or HS (BITE) as covariate did not reveal significant differences between morphs for any of the performance traits (Tables 1 and 2). There was, nevertheless, a significant effect of HS on BITE and marginally significant SVL on CLIMB, but the effect did not differ between morphs (Table 2).

3.3. Associations between Morphology and Performance

Two-block partial least-squares regression revealed a significant association between BITE and head morphology that was present in all five colour morphs (together and separately Tables A2–A7 and Table 3, Figure 3). Lizards with bigger heads exhibited stronger bite forces (Figure 3). Two-block partial least-squares regression also revealed a significant association between CLIMB and limb, trunk and body length when considering all morphs together (Tables 3 and A2, Tables A3–A7). When investigating morphs separately, the two-block partial least-squares regression only maintained the significant association between CLIMB and morphological traits for the white morph (Table 3, Figure 4, Tables A2–A7). Separate morph analysis also revealed a significant association between SPRINT and morphological traits in the white morph but not in other morphs (Table 3, Figure 4, Tables A2–A7). White morph climbing speed increased with limb length and snout vent length, while sprint speed increased especially on the account of trunk and snout vent length (Figure 4).

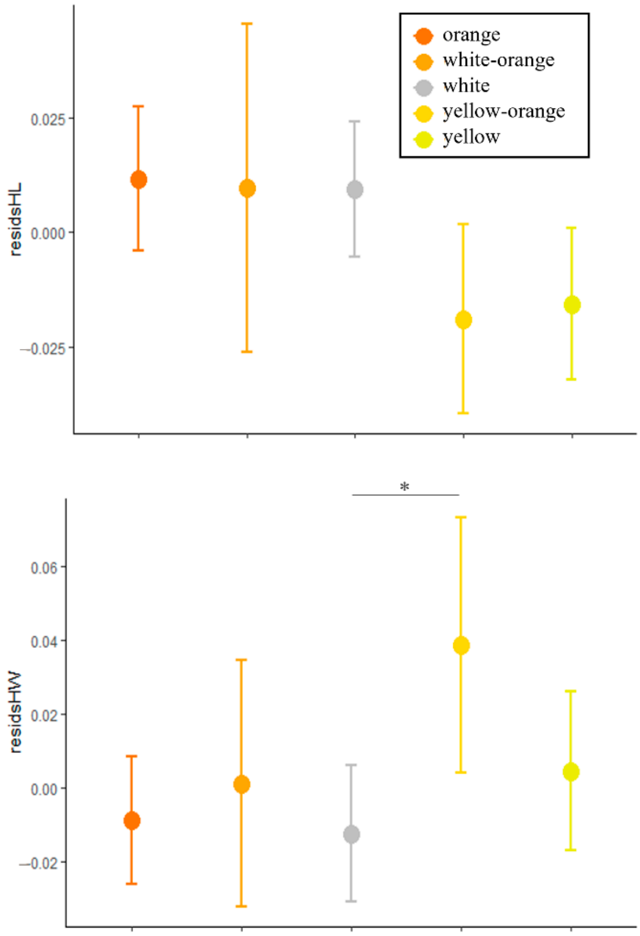

Figure 2. Variation across morphs of *Podarcis muralis* in residuals of head length (HL, top), and residuals of head width (HW, bottom). Points represent means, and vertical bars denote 95% confidence intervals. Horizontal bar with asterisk represents the significant pairwise comparison.

Table 3. Results of two-block partial least squares (PLS) of the association between performance and morphology traits, and between physiology and morphology and performance traits for each colour morph of *Podarcis muralis*. r(PLS): correlation of pair association, *p*: corresponding *p*-value. Significant effects are marked in bold. W-O and Y-O indicate the white-orange and yellow-orange intermediate morphs respectively. See Materials and Methods for variable abbreviations.

	All		**Orange**		**White**		**Yellow**		**W-O**		**Y-O**	
	$\mathbf{r_{(PLS)}}$	***p***	$\mathbf{r_{(PLS)}}$	***p***	$\mathbf{r_{(PLS)}}$	***p***	$\mathbf{r_{(PLS)}}$	***p***	$\mathbf{r_{(PLS)}}$	***p***	$\mathbf{r_{(PLS)}}$	***p***
BITE:morph	0.772	**0.001**	0.81	**0.001**	0.75	**0.001**	0.81	**0.001**	0.95	**0.002**	0.83	**0.008**
SPRINT:morph	0.228	0.129	0.41	0.200	0.64	**0.006**	0.27	0.702	0.75	0.077	0.45	0.450
CLIMB:morph	0.266	**0.043**	0.32	0.448	0.55	**0.030**	0.24	0.798	0.50	0.539	0.56	0.201
MANO:morph	0.135	0.602	0.34	0.430	0.36	0.392	0.28	0.686	0.76	0.075	0.56	0.227
PMA26:morph	0.152	0.362	0.28	0.346	0.21	0.647	0.27	0.469	0.16	0.965	0.42	0.354
PMA31:morph	0.52	0.944	0.13	0.875	0.12	0.933	0.34	0.301	0.19	0.949	0.26	0.704
PMA36:morph	0.046	0.952	0.16	0.765	0.16	0.812	0.23	0.668	0.05	0.999	0.48	0.217
CAT:morph	0.141	0.432	0.20	0.648	0.16	0.794	0.19	0.768	0.26	0.898	0.15	0.913
PMA26:perf	0.205	0.434	0.45	0.276	0.36	0.606	0.12	0.981	0.59	0.676	0.51	0.380
PMA31:perf	0.174	0.570	0.46	0.259	0.24	0.884	0.37	0.430	0.52	0.791	0.41	0.603
PMA36:perf	0.194	0.471	0.47	0.222	0.27	0.811	0.29	0.647	0.59	0.676	0.37	0.714
CAT:perf	0.186	0.497	0.43	0.371	0.25	0.844	0.34	0.522	0.57	0.704	0.35	0.747

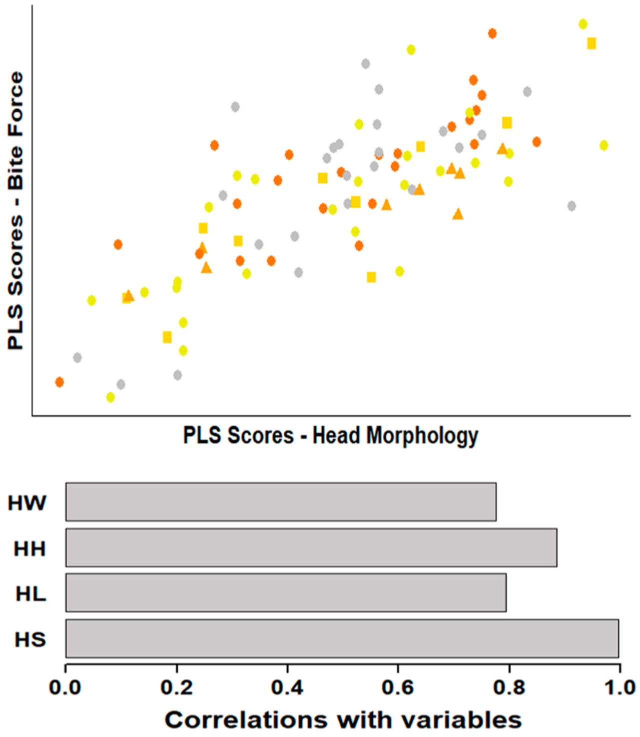

Figure 3. Scatterplot of individual *Podarcis muralis* scores obtained from partial least-squares (PLS) analysis between head morphology (head length, HL; head width, HW; head height, HH; head size, HS) and bite force. Bar plots bellow the morphology axis represent the correlations observed between that axis and bite force.

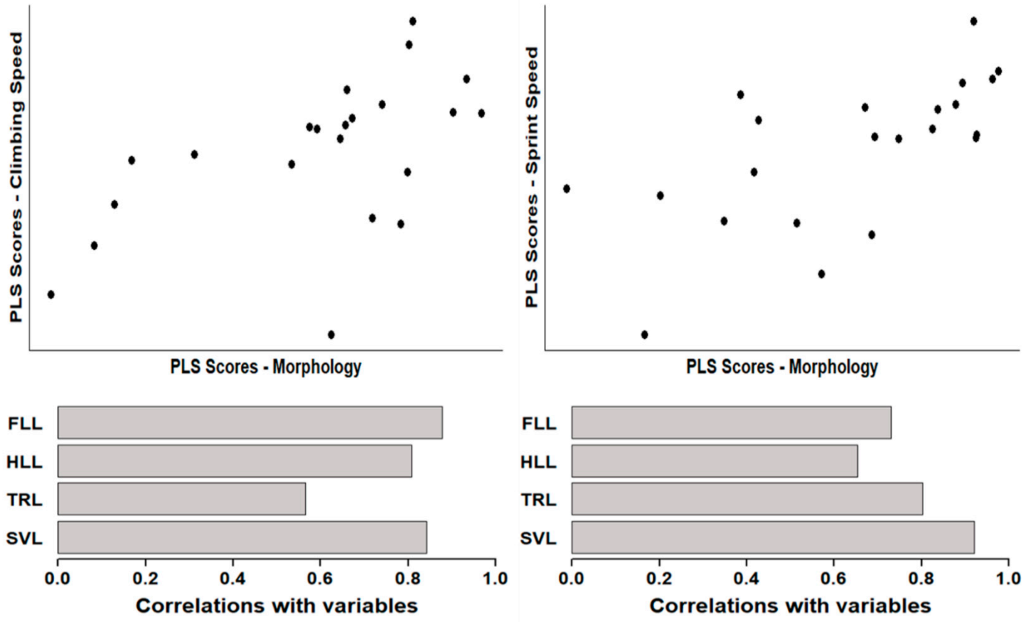

Figure 4. Scatterplot of individual *Podarcis muralis* scores obtained from partial least-squares (PLS) analysis between morphological traits (trunk length, TRL; forward limb length, FLL; hind limb length, HLL; snout-vent length, SVL) and climbing speed (**left**), sprint speed (**right**). Bar plots below each scatterplot represent the correlation observed between morphological traits and the corresponding PLS vector.

3.4. Metabolism and Antioxidant Capacity

All morphs shared similar metabolic and antioxidant capacities (Table 1). ANCOVA comparisons using SVL as covariate did not reveal significant differences between morphs for any of the physiological (PMA and CAT) traits (Table 2).

3.5. Associations between Physiology and Morphology or Performance

Two-block partial least-squares regression did not reveal a significant association between any physiology trait and morphology or performance in any of the morphs (together or separately; Table 3).

4. Discussion

In this study, despite the robust sample size and multivariate analysis, we found only a weak to no polymorphic pattern in morphology, performance, and physiology between the three pure colour morphs and the two mosaic morphs in *Podarcis muralis* population from the southern Pyrenees. Morphological differences between morphs exist but are subtle and consist mainly of variations in head length, with yellow and yellow-orange lizards having smaller heads compared to the other colour morphs. As with other wall lizards, head size and biting power are strongly linked, and this can be observed here both between morphs and within morphs. On the other hand, limb and body morphology and locomotor performance (sprinting and climbing) appear to be differentially related among morphs, with only the white morph showing a significant relationship. Finally, changes in biochemical indicators of cellular metabolism and antioxidant capacity appeared to be largely independent of morphology and performance.

Our integrative approach, incorporating several relevant functional traits, provided some new insights into the relationship between morphology and locomotor performance. Namely, the white morph was the only one that showed a relationship between morphology and sprinting and climbing, whereas the other morphs did not show such a relationship with the same statistical strength. Therefore, a stronger selection pressure on whole-organism performance with corresponding effects on morphological traits of biomechanical relevance to these functions might have acted only in the white individuals, possibly to fulfill certain ecological and social roles. Another possibility is that variability in morphological and performance traits is higher in white males—the white morph, resulting in significant associations between limb and body/trunk morphology and sprint and climbing speed, whereas other morphs have more uniform expression of morphology and performance traits that mask any association. At this point, it is difficult to provide conclusive evidence on the subjacent mechanisms, although interaction of hormones with growth has already been suggested elsewhere [73]. The relationship between morphological traits and performance was proposed by [17] under the ecomorphological paradigm. Our detailed examination of morphological correlations with performance across all morphs reveals a similar set of morphological variables that enhance individual locomotive driver performance. Indeed, there is no trade-off between sprinting and climbing, which has been previously reported in other *Podarcis* sp. [20,60]. The only exception was trunk length, where individuals with longer trunks showed higher sprinting performance. Trunk length is known to improve body flexibility for lateral bending [74,75], increase lateral undulation, and maximize stride length [76]. However, it is important to note that we were unable to detect a difference between morphs when examining performance differences. Similarly, when comparing colour morphs of (northern) Pyrenean *P. muralis*, Zajitschek and coworkers [27] did not detect any performance differences, but because they characterized coloration in percentages, they found that lizards with relatively more red (i.e., orange) coloration performed worse than individuals with less red coloration. This suggests that variation within morphs is considerable and likely masks functional relationships. We did not quantify the colouration of the lizards here because an earlier study in the same populations found good correspondence between visual assignment and spectrometric measurements [49]. Nevertheless, separation of morphs based on more quantitative criteria (for instance: spectrophotometric), rather than based on human vision alone, could lead to different results since this method may overlook subtle colour variation in our dataset. In the future, the ecomorphological paradigm should be studied in populations from different environments to explore variability in expression and associations between morphology and performance and whenever possible quantification of colouration should be included in the analysis.

The relationship between head morphology and bite force was confirmed at the species level, but we could not detect a difference between morphs. A close relationship between head morphology and bite force has already been found in other wall lizards, e.g., [20,24]. Furthermore, habitat use has been shown to be an important determinant of macroevolutionary variation in head shape, but not in body size or limb length in *Podarcis* sp. This suggests that it may be easier to find differences in head traits than in limb traits from an ecomorphological perspective in this genus. However, when head morphology and bite force were considered separately, only one head trait (head length) was significantly different between colour morphs, with yellow and yellow-low orange individuals having shorter heads than the other morphs, but no significant differences were found in bite force between colour morphs (as previously reported by [12]). Our findings of no significant morphological or bite differences between morphs are at odds with previous results for *P. muralis* and other *Podarcis* sp. For example, in *P. muralis* from the northern Pyrenees, orange lizards were larger and had larger heads [77]. Similarly, orange males of *P. melisellensis* have, on average, a longer snout length and larger heads than white or yellow males [22]. This is also reflected in the fact that orange males of *P. melisellensis* have a higher biting force [22,23]. A previous study conducted in the same population of *P. muralis* as the one used here did not focus on head morphology but included two measures of body size (SVL and body mass) to calculate body condition index (BIC) and measured bite force. In this study, only marginal significant differences between morphs in BIC were found in the larger white lizards and no differences in bite force were found [12]. The latter is in agreement with our present results. Similarly, in the Italian population of *P. muralis*, no obvious differences were found between morphs in male morphology [47], which is comparable to our study. This suggests that the morphological signature of colour polymorphism in *Podarcis* species, if present, is not universal but varies among populations and species.

The lack of morphological differentiation together with the similarity of performance traits suggests that the morphs in our study perform their behaviour in parallel with the ecological aspects of their niche (feeding, escape from predators, mating, territoriality). This is somewhat consistent with several similarities in ecology found between *P. muralis* morphs in other studies. For example, in natural sympatric populations in the Pyrenees, no differences were found between morphs in terms of site fidelity, territory size or spatial overlap of males and females [78]. Similarly, colour morph was irrelevant to sociosexual behaviour, habitat, and reproductive success [78,79]. Any ecomorphological trait (head, limbs, boot) that improves reproductive success could also be used to escape from predators or capture prey, so one would expect differences in ecological traits among morphs to be reflected in their morphology and performance traits. In most cases, however, orange and red colours are thought to be most effective at attracting attention in most lighting conditions and backgrounds in natural habitats. Increased visibility may contribute to the cost of increased detection by predators [80] and we might expect these morphs to have greater running, climbing, and maneuvering ability. In addition, the partial divergence in microhabitat use found in orange morph compared to other morphs in *P. muralis* [8] could also contribute to differentiation at the level of morphology and performance. As this prediction was not supported here or in other studies, it is possible that this is not the case or that the orange morph is making other behavioural adaptations not accounted for in these performance tests to escape predators (but see [49]). Interestingly, specific behavioural findings on the very same lizards used in our study showed that yellow individuals that were not under predation pressure exhibited more voluntary movements and explorations, especially at the beginning of the experiment [53]. This suggests that yellow lizards are more exposed to a visual predator and do not compensate by having a higher escape speed (in all other morphs) or a different microhabitat (in all morphs except orange). Considering the low abundance of yellow morphs in the Pyrenees [46,48,81], this might suggest that the maintenance of these morphs is based on the search for new resources or mating opportunities rather than on their defence [53,54].

Contrary to initial expectations, the measured levels of metabolic and antioxidant capacity in this study showed no differences between morphs. The metabolic capacity measured by our biochemical assay provides information on the maximum potential metabolic capacity [32,43]. This has been previously linked, for example, to adaptation to low or high altitude environments in several species pairs of ectothermic groups, including lizards [82]. Metabolic capacity can also vary within a species (between different populations) in ectotherms, suggesting a potential for response to variable environmental conditions as a local adaptation or plasticity [33,83]. In our population, lizards share general environmental conditions because they occur sympatrically and were collected in a relatively small area. This may explain why we found no metabolic response. The subtle differences in microenvironmental conditions that exist between the orange morph and the rest of the animals in this population [7] are apparently not large enough to affect cell metabolism.

Compared to another *P. muralis* population from Slovenia [32], the potential metabolic activity was lower, especially at higher temperatures (e.g., the PMA from the Pyrenees measured at 31 °C was 30% lower than the PMA from Slovenia measured at 33 °C). First of all, this result is a novelty in the study of intraspecific variability of metabolism in lizards, which is very important because for many terrestrial organisms there is still no information on metabolic adaptation in wild populations [84,85]. The finding of differences in PMA between *P. muralis* in the Pyrenees and in Slovenia is somewhat expected, as both populations live at different altitudes (at about 1300 m a.s.l. in the Pyrenees and at about 800 m a.s.l. in Slovenia) and under different climatic conditions, and also belong to different phylogenetic lineages [86]. The observed lower PMA values in *P. muralis* in the Pyrenees could reflect an adaptation to climatic conditions that allow the lizards a longer period of activity than in the northern lineages, or it could also be related to other differences in ecology and life-history traits, but this is currently unexplored.

In addition, our analysis also examined correspondences between metabolic capacity and running speed in morphs. The population-level analysis revealed no correspondence between performance and metabolic rate. These results are similar to those of a recent study of locomotor performance and metabolism in snakes, which measured oxygen consumption and maximum activity of two enzymes (lactate dehydrogenase and citrate synthase), which also showed no correspondence with sprint speed [87]. So far, performance characteristics and properties of metabolism in reptiles do not show obvious signs of coupling, but further studies on this aspect are needed.

We also measured antioxidant capacity, which is an indicator of the oxidative stress processes taking place in the organism. Reactive oxygen species (ROS) are a normal by-product of reactions that occur during metabolism and are normally eliminated by antioxidant mechanisms, except when the production of ROS during metabolism exceeds the capacity of antioxidant mechanisms, which probably occurs under stress conditions [37]. In addition, some stress factors (e.g., UV radiation, toxins, etc.) may also directly trigger the production of ROS. Higher stress level would lead to higher antioxidative mechanisms [88], which we measured in our study using CAT activity, but found no differences between morphs, suggesting that stress level does not differ between them. Sacchi and colleagues [89] show that morphs might invest differently in immunocompetence. Since immunocompetence is responsible for fighting diseases or parasites, lizards with different immunocompetence should be exposed to different levels of stress [90], which could be reflected in differences in antioxidant levels. However, our results do not suggest this. The lizards in the populations studied may not be exposed to high levels of stress because they live in a natural environment that is highly favourable for the species. In a more disturbed environment, differentiation could also be observed in physiology [77,90]. For example, Calsbeek and collaborators [77] also found physiological and immunological differences between morphs of *P. muralis*, and similar results were obtained for the closely related *P. melisellensis* [22,23,91]. Here, the lack of differences in metabolic and antioxidant capacity suggests variable plasticity of these traits between populations and between species.

In summary, even with a highly integrated design, strict experimental protocols and large sample sizes, the interpretation of the variation in the expression of different life-history traits studied in the context of colour polymorphisms revealed a challenging task because of the different selection forces and background mechanisms. The fact that we found little variation in morphology, no variation in locomotion and physiology, and no clear distinction between pure morphs and mosaic morphs, suggests that ecological differentiation may not be forced, and hence provide little information on the background mechanisms that maintain colour polymorphism in this study population. In addition, when testing associations between different life-history traits, we looked for differential selection pressure on the level of associations and again found no clear answer. Associations were found in part between morphology and performance, but not between morphology and physiology or performance and physiology. Although differences in associations might in turn contribute to understanding the existence of colour morphs, we did not find answers here either. Future efforts could focus more on behaviour and other unexplored areas, including the possibility of selection forces for hybridization in these populations.

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Data Availability Statement: The data presented in this study are openly available in [Zenodo, https://doi.org/10.5281/zenodo.6013025].

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Appendix A

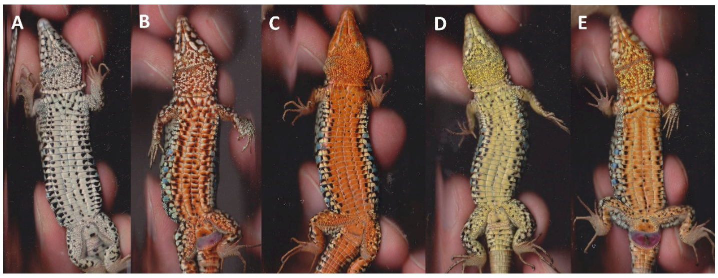

Figure A1. Colour morphs of *Podarcis muralis* from the study site in southern Pyrenees: (**A**) = white, (**B**) = white-orange, (**C**) = orange, (**D**) = yellow, (**E**) = yellow-orange.

Appendix B

Table A1. Specification of traits used in two-block partial least squares (PLS) associations (results given in Table 3). See Materials and Methods for variable abbreviations.

	1st Block	**2nd Block**
BITE:morphology	BITE	HW, HH, HL, HS
SPRINT morphology	SPRINT	FLL, HLL, TRL, SVL
CLIMB:morphology	CLIMB	FLL, HLL, TRL, SVL
MANO:morphology	MANO	FLL, HLL, TRL, SVL
PMA26:morphology	PMA26	TRL, SVL, HS
PMA31:morphology	PMA31	TRL, SVL, HS
PMA36:morphology	PMA36	TRL, SVL, HS
CAT:morphology	CAT	TRL, SVL, HS
PMA26:performance	PMA26	BITE, SPRINT, CLIMB, MANO
PMA31:performance	PMA31	BITE, SPRINT, CLIMB, MANO
PMA36:performance	PMA36	BITE, SPRINT, CLIMB, MANO
CAT:performance	CAT	BITE, SPRINT, CLIMB, MANO

Appendix C

Loadings of two-block partial least squares (PLS) of the association between performance and morphology traits, and between physiology and morphology and performance traits for all colour morph together and each colour morph of *Podarcis muralis* separately. r(PLS): correlation of pair association, *p*: corresponding *p*-value. Significant effects are marked in bold. See Materials and Methods for variable abbreviations.

Table A2. Morphs all together.

1st Block	**2nd Block**													
	HW	**HH**	**HL**	**HS**	**SVL**	**TRL**	**FLL**	**HLL**	**BITE**	**SPR**	**CLI**	**MAN**	$r_{(\mathrm{PLS})}$	p
BITE	0.775	0.885	0.793	0.997									0.772	**0.001**
SPRINT					0.837	0.691	0.832	0.784					0.228	0.129
CLIMB					0.795	0.544	0.894	0.813					0.266	**0.043**
MANO					0.808	0.784	0.542	0.866					0.135	0.602
PMA26				0.353	0.85	0.607							0.152	0.362
PMA31				0.692	0.924	0.876							0.52	0.944
PMA36				0.821	0.931	0.867							0.046	0.952
CAT				0.886	0.899	0.855							0.141	0.432
PMA26									0.657	0.589	0.681	0.683	0.205	0.434
PMA31									0.758	0.598	0.709	0.458	0.174	0.57
PMA36									0.541	0.781	0.75	0.59	0.194	0.471
CAT									−0.775	−0.486	0.137	0.178	0.186	0.497

Table A3. Orange morph.

1st Block	**2nd Block**													
	HW	**HH**	**HL**	**HS**	**SVL**	**TRL**	**FLL**	**HLL**	**BITE**	**SPR**	**CLI**	**MAN**	$r_{(\mathrm{PLS})}$	p
BITE	0.83	0.660	0.767	0.996									0.81	**0.001**
SPRINT					0.414	0.108	0.955	0.839					0.41	0.200
CLIMB					0.923	0.900	0.351	0.681					0.32	0.448
MANO					0.458	0.196	0.995	0.754					0.34	0.430
PMA26				0.924	0.941	0.910							0.28	0.346
PMA31				0.728	0.925	0.945							0.13	0.875
PMA36				0.898	0.950	0.922							0.16	0.765
CAT				0.919	0.950	0.906							0.20	0.648
PMA26									0.704	0.225	0.487	0.736	0.45	0.276
PMA31									0.362	0.183	0.792	0.748	0.46	0.259

Table A3. *Cont.*

1st Block	2nd Block													
	HW	**HH**	**HL**	**HS**	**SVL**	**TRL**	**FLL**	**HLL**	**BITE**	**SPR**	**CLI**	**MAN**	$r_{(PLS)}$	p
PMA36									0.613	0.380	0.575	0.796	0.47	0.222
CAT									−0.545	−0.353	0.720	0.163	0.43	0.371

Table A4. White morph.

1st Block	2nd Block													
	HW	**HH**	**HL**	**HS**	**SVL**	**TRL**	**FLL**	**HLL**	**BITE**	**SPR**	**CLI**	**MAN**	$r_{(PLS)}$	p
BITE	0.864	0.889	0.771	0.996									0.75	**0.001**
SPRINT					0.921	0.802	0.731	0.653					0.64	**0.006**
CLIMB					0.841	0.565	0.878	0.808					0.55	**0.030**
MANO					−0.369	−0.023	−0.780	−0.951					0.36	0.392
PMA26				0.768	0.955	0.499							0.21	0.647
PMA31				0.845	0.981	0.608							0.12	0.933
PMA36				0.672	0.661	0.984							0.16	0.812
CAT				0.885	0.881	0.921							0.16	0.794
PMA26									−0.868	0.017	0.258	0.209	0.36	0.606
PMA31									0.851	0.342	−0.154	−0.295	0.24	0.884
PMA36									0.709	0.549	−0.185	0.489	0.27	0.811
CAT									0.016	0.305	−0.268	0.864	0.25	0.844

Table A5. Yellow morph.

1st Block	2nd Block													
	HW	**HH**	**HL**	**HS**	**SVL**	**TRL**	**FLL**	**HLL**	**BITE**	**SPR**	**CLI**	**MAN**	$r_{(PLS)}$	p
BITE	0.662	0.917	0.842	0.997									0.81	0.001
SPRINT					0.516	0.894	0.249	0.656					0.27	0.702
CLIMB					0.791	0.621	0.717	0.835					0.24	0.798
MANO					0.467	0.374	0.839	0.928					0.28	0.686
PMA26				0.783	0.997	0.400							0.27	0.469
PMA31				−0.200	−0.659	0.369							0.34	0.301
PMA36				0.657	0.346	0.841							0.23	0.668
CAT				0.011	0.052	0.944							0.19	0.768
PMA26									−0.578	0.498	0.240	−0.058	0.12	0.981
PMA31									−0.289	0.419	0.794	0.808	0.37	0.430
PMA36									0.931	0.646	0.313	−0.011	0.29	0.647
CAT									0.097	−0.332	−0.809	−0.919	0.34	0.522

Table A6. White−Orange morph.

1st Block	2nd Block													
	HW	**HH**	**HL**	**HS**	**SVL**	**TRL**	**FLL**	**HLL**	**BITE**	**SPR**	**CLI**	**MAN**	$r_{(PLS)}$	p
BITE	0.772	0.904	0.397	0.989									0.95	0.002
SPRINT					−0.443	−0.052	−0.932	−0.620					0.75	0.077
CLIMB					0.966	0.759	0.550	0.572					0.50	0.539
MANO					0.354	0.806	−0.318	0.324					0.76	0.075
PMA26				0.959	0.751	0.336							0.16	0.965
PMA31				0.895	0.863	0.681							0.19	0.949
PMA36				0.836	0.936	0.702							0.05	0.999
CAT				0.826	0.933	0.735							0.26	0.898
PMA26									−0.258	0.951	0.042	−0.645	0.59	0.676
PMA31									0.017	0.962	0.450	−0.666	0.52	0.791

Table A6. *Cont.*

1st Block	2nd Block													
	HW	HH	HL	HS	SVL	TRL	FLL	HLL	BITE	SPR	CLI	MAN	$r_{(PLS)}$	p
PMA36									−0.177	0.976	0.459	−0.647	0.59	0.676
CAT									0.232	0.862	0.680	−0.540	0.57	0.704

Table A7. Yellow−Orange morph.

1st Block	2nd Block													
	HW	HH	HL	HS	SVL	TRL	FLL	HLL	BITE	SPR	CLI	MAN	$r_{(PLS)}$	p
BITE	0.721	0.850	0.853	0.996									0.83	0.008
SPRINT					0.449	0.658	0.649	0.987					0.45	0.450
CLIMB					0.025	0.356	0.453	0.815					0.56	0.201
MANO					0.954	0.879	0.888	0.567					0.56	0.227
PMA26				0.916	0.937	0.949							0.42	0.354
PMA31				0.913	0.935	0.951							0.26	0.704
PMA36				0.955	0.969	0.906							0.48	0.217
CAT				0.964	0.965	0.898							0.15	0.913
PMA26									0.379	0.972	0.915	0.914	0.51	0.380
PMA31									0.451	0.955	0.912	0.925	0.41	0.603
PMA36									0.009	0.969	0.788	0.825	0.37	0.714
CAT									0.556	0.863	0.764	0.973	0.35	0.747

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