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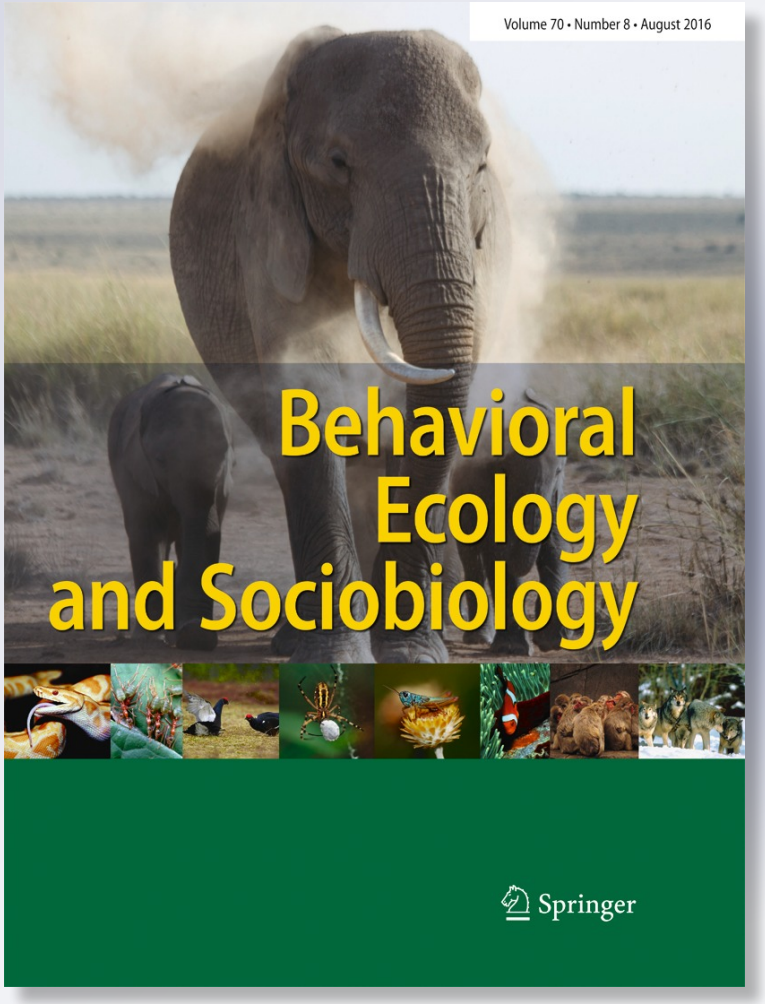

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ORIGINAL ARTICLE

Thermal dependence of signalling: do polymorphic wall lizards compensate for morph-specific differences in conspicuousness?

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Abstract
Selection for signal efficacy (detectability) is an important factor driving the evolution of chromatic signals. Communication theory predicts that colour signals should evolve to show those properties that maximize their conspicuousness to receivers in their own visual environment. In the ventrally polymorphic lizard *Podarcis muralis*, visual modelling has shown morph-specific differences in chromatic conspicuousness (orange > yellow > white). Although this suggests that morphs may incur different detectability costs, the differences in conspicuousness could be compensated behaviourally if individuals of the more conspicuous morphs adopted postures that made their colour patches less visible. We quantified the degree of exposure of the lizard ventral and ventrolateral coloration in the field to investigate the relationship between body posture and colour morph. We used a classification based on four lizard postures, from ventral surface completely hidden to full exposure of the ventral and ventrolateral colour patches (when lizards extend their forelegs and raise the head). As these postures may have consequences for thermoregulation, we also recorded substrate and lizard body temperatures using a thermographic camera. Results did not reveal differences among morphs in the frequency with which they adopt postures that expose their colour patches. In contrast, we found a strong relationship between body temperature and lizard posture. Overall, our results support the view that, regardless of colour morph, perching wall lizards adopt the elevated postures that maximize exposure of their ventral colour patches only when their body temperature is high enough to allow for an efficient predator avoidance response.

Significance statement
Selection for effective communication favours flashy, highly conspicuous coloration, but conspicuousness also makes colour signals more detectable to unintended receivers (e.g. predators). Some animals offset the costs associated with conspicuous coloration by evolving compensatory traits. In the lizard *P. muralis*, ventral colour morphs differ in conspicuousness and we hypothesized that the most conspicuous morphs might compensate for their increased conspicuousness by adopting postures that minimize exposure of their conspicuous colour patches. Results show that the morph-specific differences in conspicuousness are not compensated behaviourally. In contrast, we found a strong relationship between body temperature and lizard posture, suggesting that lizards, regardless of colour morph, adopt postures exposing their conspicuous colour patches only when their body temperature allows for an efficient predator avoidance response.

Keywords Detectability · Colour polymorphism · Signal efficacy · Thermal ecology · Thermography · Visual ecology

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Introduction

Signal design reflects the outcome of a trade-off between conflicting selection pressures. Effective communication often selects for showy, exaggerated, highly conspicuous signals, but conspicuousness makes the signaller more vulnerable to potential eavesdroppers such as competitors, predators and parasitoids. It has been suggested that animals may be able to reduce the risk of eavesdropping while simultaneously maintaining the ability to communicate effectively by evolving compensatory traits (Tomkins et al. 2005; Oufiero and Garland 2007; Swallow et al. 2009; Husak and Swallow 2011). Compensation may involve novel or modified structures, physiology or behaviour (Husak et al. 2015). Most available examples of behavioural compensation for conspicuous signals consist of changes in antipredator behaviour. For example, field crickets (*Gryllus integer*) with longer, more conspicuous calling bouts behave more cautiously in two tests of predator avoidance (Hedrick 2000). Similarly, male túngara frogs (*Engystomops pustulosus*) cease vocalizing when they detect the presence of a bat or a bat model (Tuttle et al. 1982).

Flashy, conspicuous coloration is considered costly because it makes its bearers more detectable to eavesdroppers. Indeed, several studies with lizards have shown that conspicuous coloration impairs survival through increased predation risk (Macedonia et al. 2002; Kwiatkowski and Guyer 2003; Stuart-Fox et al. 2003; Husak et al. 2006; Marshall et al. 2015). For ectothermic animals that need to thermoregulate, such as lizards, conspicuous coloration is particularly problematic because attaining adequate body temperatures often requires that animals bask in exposed locations or adopt body postures that make them more visible to predators (Huey 1982; Stuart-Fox and Moussalli 2009). Evidence of behavioural compensation of colour conspicuousness has been found in desert lizards: in some species, individuals compensate behaviourally for the lack of background matching by maintaining a close distance to shelter and faster escape responses (Norris 1967).

Many lizards are relatively cryptic dorsally but have conspicuous colour patches on the lateral and ventral body surfaces (Cooper and Greenberg 1992; Olsson et al. 2013). These colour patches are used for signalling, and they are more or less visible depending on the lizard's posture. In particular, basking, perching and resting lizards adopt a range of body postures that differ in the extent to which they expose the ventral and lateral body surfaces. A prostrate or body down posture conceals the colour patches and makes them almost invisible to other individuals. In contrast, postures in which the body is partially or fully raised off the substrate expose the lizard's ventral and lateral surfaces and increase their detectability to potential eavesdroppers. As lizards are ectothermic organisms, adoption of certain body postures may be strongly constrained by the thermal environment (Greenberg 1976; Muth 1977). For example, body down postures maximize heat transfer from hot substrates through thigmothermy (conduction; Bauwens et al. 1999). In contrast, the elevated postures typical of many perching lizards have been associated with heliothermic basking (heat gain by radiation; Brattstrom 1971) or, more often, with the need to avoid overheating when the substrate attains high temperatures (Greenberg 1976; Sannolo et al. 2014). Due to the thermal dependence of antipredator behaviour (Rand 1964; Hertz et al. 1982; Huey 1982), displaying conspicuous patches at times when the lizards' temperatures are suboptimal may increase predation costs due to inefficient flights (Avery 1991).

In some colour-polymorphic species, continuous or discrete ventral colour variants coexist within the same population (e.g. Sinervo and Lively 1996; Vercken et al. 2007; Lattanzio et al. 2014). As the colour variants differ in their conspicuousness (e.g. Teasdale et al. 2013; Pérez i de Lanuza and Font 2015), they may incur different detectability costs. However, the negative impact of conspicuous coloration could be alleviated if individuals compensated behaviourally for the differences in detectability (Forsman and Appelqvist 1999; Journey et al. 2013). One possibility that has received little attention in the literature is that lizards of the more conspicuous colour variants might compensate for their increased detectability by adopting body postures that make them less visible to predators. To test this hypothesis, we collected data on coloration, body temperature, thermal environment and posture of basking lizards in a colour-polymorphic population of the lacertid *Podarcis muralis*. Ventral coloration of adult lizards in this population is white, yellow or orange. In addition to these three pure single-colour morphs, there are also mixed-colour individuals (white-orange and yellow-orange). The colour variants are discrete and remain stable after the lizards reach sexual maturity, suggesting a simple Mendelian system of inheritance (Pérez i de Lanuza et al. 2013). Yellow and, especially, orange ventral patches are the most chromatically conspicuous (i.e. provide more chromatic contrast against the ventrolateral ultraviolet (UV)-blue patches and against natural backgrounds; see below) to the visual systems of conspecific lizards and potential predators (Pérez i de Lanuza and Font 2015). For some colour combinations, the white morph is more achromatically conspicuous than the orange morph, but in contrast to chromatic conspicuousness, there are no general trends in achromatic conspicuousness (Pérez i de Lanuza and Font 2015). Thus, focusing on chromatic conspicuousness, we expected that lizards with orange and yellow ventral patches would adopt postures that maximize exposure of their conspicuous colour patches less often than lizards of the white colour morph.

As we pointed out above, we expected a strong thermal dependence in the exposure of the conspicuous patches that should affect all the colour morphs. Therefore, we also studied the relationship between lizard temperature and posture.

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Lizard body temperature depends on ambient temperature and on the ability to thermoregulate. European lacertid lizards, such as *P. muralis*, are considered efficient thermoregulators that, depending on circumstances, warm up by radiation (i.e. heliothermy) and/or conduction (i.e. thigmothermy) (Braña 1991; Martín-Vallejo et al. 1995; Castilla et al. 1999; Belliure and Carrascal 2002). In our study population, *P. muralis* rely on different heat sources at different times during the daily cycle. Early in the morning in spring and summer, lizards behave as typical shuttling heliotherms, whereas later in the day, when substrate temperatures are high, they control their body temperature by a combination of heliothermy and thigmothermy. Although air and substrate temperatures are often correlated (e.g. Powell and Russell 1985), air temperature is more labile than substrate temperature. Therefore, we focused on the relationship between body and substrate temperatures to test if thermal constraints determine the adoption of body postures that hide or expose the conspicuous colour patches of *P. muralis*.

Materials and methods

Study population

The study population inhabits several rocky habitats in the East-West oriented Cerdanya valley, Eastern Pyrenees (42° 37′ N, 1° 56′ E). The habitat includes dry-stone walls oriented to the South and isolated granite boulders surrounded by sparse vegetation dominated by *Fraxinus excelsior*, *Crataegus monogyna* and *Rosa canina*. The stone walls are mainly constructed with blocks of granite, but schist is also present. The main lizard predator in our population is the diurnal actively foraging snake *Hierophis viridiflavus* (family Colubridae), with large eyes that detect preys visually often from a lateral position and at short distances, but other potential visual predators (i.e. raptors) are common in this area (Pérez i de Lanuza and Font 2015).

In non-white males, the yellow and orange coloration extends over the entire ventral surface, but in females, it is restricted to the gular region. In addition, males and, to a smaller extent, females present conspicuous UV-blue patches on some of their outer ventral scales (OVS). The UV-blue patches of males are larger, more reflective and more UV-biased than those of females (Pérez i de Lanuza et al. 2013, 2014).

Males and females use rock walls and boulders to bask, perch, feed and socially interact (Pérez i de Lanuza et al. 2013). These are covered by lichens and moss, the latter being often selected as substrate by basking lizards. The ventral and ventrolateral conspicuous coloration is displayed by means of stereotyped body postures during social interactions, mainly by males. However, these colour patches also become visible in other contexts, likely acting as assertion or broadcast signals, and their degree of exposure depends on the postures adopted by the lizards (see examples in Fig. 1 and in Fig. 1 of Pérez i de Lanuza and Font 2015; see details below).

Posture classification

With the aim of assessing whether the differences in chromatic contrast result in actual differences in detectability, we quantified the degree of exposure of the ventral and ventrolateral coloration of *P. muralis* in the field. We used a scale based on four lizard postures to quantify the exposure of the conspicuous colour patches, from a posture in which the ventral surface is completely hidden (posture 1; e.g. when lizards are resting or thermoregulating through thigmothermy; termed prostrate or thigmothermic basking, Bartholomew 1966; Brattstrom 1971) to a posture in which the display of the conspicuous colour patches is maximized (posture 4; when lizards extend their forelegs and elevate the head, exposing the ventrolateral and the ventral colour patches; termed vigilance posture by Avery 1991). Each lizard was assigned a score from 1 (lowest) to 4 (highest) depending on its posture when first detected by the observer. Figure 1 shows examples and Table 1 the full description of the postures.

Field observations

Lizards were observed in the field with short focus binoculars (Papilio 8.6 × 21, Pentax, Tokyo, Japan) to determine their colour morph, posture, sex (determined based on head and body proportions and colour pattern), age (i.e. size class) and substrate type (i.e. granite, schist, moss or other types of substrates) on which they were found. The use of binoculars often allowed us to observe lizards before they detected us, minimizing possible observer effects. Data collection was restricted to exposed lizards that did not change their posture during observations, remaining in the same spot and in the same posture for at least 20 s. To assess the size class of lizards, we categorized lizards as adults when they were large (ca. snout-vent length (SVL) ≥56 mm) and showed fully developed coloration and body proportions. The remaining animals were classified as young adults, subadults or juveniles depending on the degree of body and colour development. To obtain a representative sample of natural morph abundance in the study population, we did not select the focal animals by morph (or other traits) but those randomly encountered during the transects. To avoid pseudoreplication, all observations were performed in the course of independent transects. Transects were conducted during spring-summer 2014 (10, 12, 13, 15, 16, 19, 21 and 27 June, and 1, 15 and 16 July) throughout the entire diurnal activity period of the lizards to encompass the variability of natural contexts. All observations

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Fig. 1 Examples of the four postures described and recorded in this study. The *top picture* shows a male on the *left* and a female on the *right* basking. The *second picture* shows a yellow female. The *third* and *fourth pictures* show two different white-orange females

were made by the same observer (GPL). It was not possible to record data blind because our study involved observation of focal animals in the field.

Thermography

As the body surface temperature of small lizards in thermal equilibrium is very close to their internal or core temperature (Luna et al. 2013), we used surface temperature as a measure of body temperature. During transects, when a lizard was located, its body temperature and the temperature of the surrounding substrates were simultaneously recorded with a still infrared camera (Fluke Ti25). For acquisition of thermographic images, we set the camera emissivity at 0.97 (Luna et al. 2013). Thermographic images were analyzed using the software provided with the camera (SmartView 2.1, Fluke). For each thermographic image, we extracted the surface temperature of lizards from three independent readings on the back (in a middle position) and calculated the mean (Tl). In addition, we obtained three independent measurements of the substrate immediately surrounding the lizard and calculated the mean (Ts).

The different postures differ in the amount of body surface in contact with the substrate. For this reason, body posture may constrain the efficacy of thermoregulation. As the efficacy with which lizards thermoregulate is crucial to attain optimal body temperatures, we calculated thermal effectiveness, which represents the extent to which body temperature is closer to the preferred temperature than is substrate temperature, using the formulas developed by Hertz et al. (1993) as per Carretero et al. (2006). We first calculated the thermal quality of the habitat (i.e. the difference between substrate temperature lizard body temperature) and thermal accuracy (i.e. the difference between lizard body temperature and the preferred temperature) as follows:

$$\text{thermal quality} = \delta ls = |(Tl - Ts)|/(Tl + Ts)$$

$$\text{thermal accuracy} = \delta lp = |(Tl - Tp)|/(Tl + Tp)$$

where Tp = 32.17 °C for adult males and 31.33 °C for adult females (averaging the Tp of pregnant and non-pregnant females), which are the preferred temperatures of *P. muralis* in a thermal gradient (Carretero 2008). Thermal effectiveness was then calculated with the following formula:

$$\text{thermal effectiveness } (E) = 1 - \delta ls/\delta lp$$

If lizards thermoregulate efficiently, they should display basking postures more often when the thermal quality of the environment is low.

Autotomized tails

With the aim to include a measure of costs related to morph conspicuousness (i.e. costs of predation and/or related to intrasexual fights), we counted the number of autotomized tails, classified by lizard colour morph and sex, from the

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Table 1 Description of the four postures recorded in the present study

Posture	Description	Colour patch exposure		
		Throat	Belly	UV-blue OVS
1	Head resting on substrate: the ventral surface of lizards, including the throat, is completely in contact with the substrate. The forelegs are approximately parallel to the substrate. The body is often flattened to increase the contact with the substrate/to maximize exposure of the dorsal surface to the sun, completely hiding the OVS.	No	No	No
2	Body down low: the head is not in contact with the substrate, making the throat coloration visible. The OVS may be partially exposed.	Moderate	No/low	moderate
3	Anterior body up (forelegs partially extended): the head is elevated showing the throat coloration. Only the hands are in contact with the substrate, and the forelegs are partially extended. The OVS are always visible, and the ventral coloration can be partially exposed.	High	Moderate	Moderate
4	Foreleg extension: the head is elevated, and the forelegs are extended showing the throat and the ventral coloration (i.e. the anterior part of the belly). The OVS and, often, the second row of ventral scales are visible from the side.	High	High	High

dataset previously collected for other studies performed on the same population (Pérez i de Lanuza et al. 2013, 2014; Pérez i de Lanuza and Font 2015). This sample encompasses 341 adult males and 192 adult females, as well as 461 juveniles, subadults and young adults without fully developed ventral coloration (i.e. SVL <56 mm; Pérez i de Lanuza et al. 2013).

Analyses

We recorded thermographic images from 558 animals. For analyses, we discarded those animals photographed on unusual substrates (e.g. trunks, concrete). We also discarded all lizards that were not classified as adults (i.e. young adults, subadults and juveniles) because their coloration may not be completely developed and the inclusion of these data could introduce bias in the results, resulting in a sample of 460 adult lizards. We performed two analyses. First, we used a generalized linear mixed model (GLMM) using the overall sample of 460 adults with body posture as the dependent variable (with a Poisson distribution) and sex, morph and substrate type as predictors (fixed factors). Second, we excluded 52 animals whose thermographic images were not of sufficiently good quality (e.g. images taken from large distances or when lizards were moving) and repeated the analyses adding body temperature and thermal effectiveness as continuous predictors. Due to the small sample size available for the yellow-orange morph (see "Results" section), we also repeated the two analyses excluding this morph. We quantified effect size calculating the *d* statistic for categorical variables and the *r* statistic for quantitative covariates and the corresponding confidence interval (CI) at 95 % (Nakagawa and Cuthill 2007).

Additionally, we tested if body temperature, substrate temperature and thermal effectiveness differ between postures, considering posture as a categorical fixed factor. As normality assumptions were not met, we used Kruskal-Wallis and Dunn post hoc tests. We also tested if colour morphs were segregated by substrate type and if tail loss frequency varied among colour morphs. As the available sample in some sex, morph and substrate type combinations was smaller than 5, we performed Fisher's exact tests to test segregation by substrate. As there exists a strong sexual dichromatism in *P. muralis* (Pérez i de Lanuza et al. 2013, 2014; Pérez i de Lanuza and Font 2015) and sexes differ in their behaviour, these analyses were performed separately for males and females. To test for differences in tail loss by morph, we used log-linear models. For this purpose, we considered only adult lizards (i.e. SVL ≥56 mm; Pérez i de Lanuza et al. 2013).

Results

Four hundred and sixty-five lizards were photographed against granite, 32 against schist, 48 against moss and 13 against other substrates (e.g. trunks, concrete). All the analyses, either including or excluding the thermal variables and the rare yellow-orange morph, gave essentially the same result: there are no differences in the postures adopted by individuals belonging to different morphs or sex (Tables 2 and S1). Figure 2 shows the effect size (i.e. *d* values for categorical factors and *r* for quantitative covariates) and 95 % CI. The statistics from the alternative analyses excluding the yellow-orange morph are not shown but produced similar results. Therefore, morphs do not differ in the frequency with which they adopt the four different postures considered here.

Body temperature was, irrespective of colour morph, strongly correlated with lizard posture (Table 2). All four postures were recorded throughout the entire range of body and substrate temperatures, but body temperatures differed among postures (Kruskal-Wallis: $\chi^2 = 33.07$; $N = 408$; $P < 0.0001$), the temperature associated to posture 1 being lower than the temperatures of the other postures (Dunn: $Z < -71.74$; $P < 0.0001$). Comparisons between postures 2, 3 and 4 were

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Table 2 Results of the generalized linear mixed model analyses excluding temperature variables (above) and including body temperature and thermal effectiveness as covariates (below)

Without temperature variables		
Sex	$F_{1,452}=2.34$	$P=0.13$
Morph	$F_{4,452}=1.10$	$P=0.36$
Substrate	$F_{2,452}=8.27$	$P<0.0001$
With temperature variables		
Sex	$F_{1,398}=2.41$	$P=0.12$
Morph	$F_{4,398}=1.86$	$P=0.16$
Substrate	$F_{2,398}=6.47$	$P=0.002$
Body temperature	$F_{1,398}=38.33$	$P<0.001$
Thermal effectiveness	$F_{1,398}=0.03$	$P=0.86$

Results from the analyses excluding the small sample of yellow-orange lizards produced similar results (data not shown)

not significant (Dunn: $Z>-11.78$; $P>0.52$). Averaging the posture of all the lizards for each 0.5 °C temperature interval from 23 to 38 °C, we found a significant positive relationship with lizard posture (Pearson correlation: $r=0.887$, $P<0.0001$, $N=30$ temperature intervals; Fig. 3). In contrast, postures did not differ in substrate temperature (Kruskal-Wallis: $\chi^2=3.71$; $N=408$; $P=0.29$), and substrate temperature was weakly correlated with lizard posture averaging the posture of all the lizards for each 0.5 °C temperature interval from 20.5 to 39 °C (Pearson correlation: $r=0.385$, $P=0.017$, $N=38$ temperature intervals). Lizard body temperature was positively correlated with substrate temperature (Spearman correlation: $r=0.556$, $P<0.0001$, $N=496$ pooling all age classes). Thermal effectiveness differed among postures (Kruskal-Wallis: $\chi^2=11.55$; $N=408$; $P=0.009$; Fig. S1), the values associated to posture 1 being slightly larger than those of the other postures (Dunn: $Z>39.23$; $0.085>P>0.014$), but there were no differences among postures 2, 3 and 4 (Dunn: $Z<9.78$; $P>0.59$).

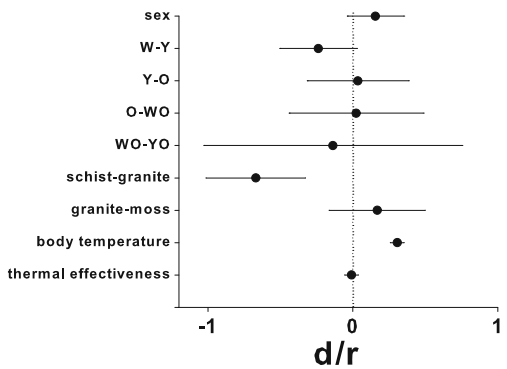

Fig. 2 Effect size and 95 % confidence intervals for paired categorical factors and quantitative covariates. Effect size is calculated using the *d* statistic for categorical factors and the *r* statistic for quantitative covariates. Morphs are represented by *W* white, *Y* yellow, *O* orange, *WO* white-orange, *YO* yellow-orange

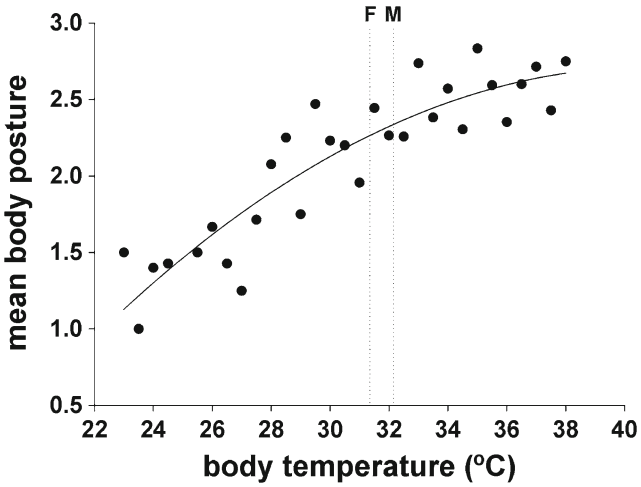

Fig. 3 Relationship between lizard body temperature and posture. Mean posture was calculated averaging the posture of all the lizards for each 0.5 °C temperature interval. The regression line was calculated with a nonlinear quadratic adjustment ($r^2=1$). *Dotted lines* indicate preferred temperatures of adult females (*F*) and adult males (*M*)

We found a significant effect of substrate type on posture (Table 2; Fig. S2). Paired comparisons indicated that lizards adopted lower postures basking on schist than on granite ($t=-3.53$; $df=398$; $P<0.0001$ in analysis considering temperature variables; $t=-3.88$; $df=452$; $P<0.0001$ in analysis without temperature variables) and marginally on moss ($t=-1.94$; $df=398$; $P=0.05$ in analysis considering temperature variables; $t=-1.89$; $df=452$; $P=0.06$ in analysis without temperature variables). Granite and moss do not differ in lizard posture ($t=0.98$; $df=398$; $P=0.33$ in analysis considering temperature variables; $t=1.58$; $df=452$; $P=0.12$ in analysis without temperature variables). Morphs were not segregated by substrate (Fisher's exact test for males: $P=0.13$; for females: $P=0.76$).

The proportion of tail losses increased with body size, and about half the lizards in our database had lost their tail at least once by the time that they acquired a fully developed ventral coloration (i.e. SVL ≥56 mm) (Fig. 4). Table 3 shows the percentage of regenerated tails grouped by sex and colour morph. The results of the log-linear model indicate a significant interaction between sex, morph and tail loss (Pearson $\chi^2=32.94$; $df=9$; $P=0.0001$) (Table 4). Yellow and orange males and females, and males in general, show more regenerated tails.

Discussion

Because adaptations often represent compromises between conflicting selective pressures, we expected that the most chromatically conspicuous colour morphs in *P. muralis* (i.e. orange and yellow) would show compensatory behaviours to alleviate costs associated with their increased conspicuousness

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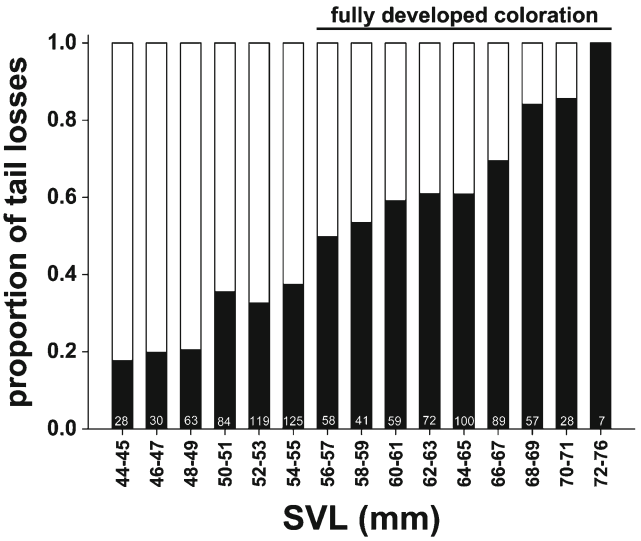

Fig. 4 Frequency of tail loss classified by lizard body size (snout-vent length, SVL). The *white portion of bars* indicates the proportion of original tails, and the *black portion of bars* indicates the proportion of autotomized/regenerated tails. Note that by the time that lizards develop their adult ventral coloration (i.e. SVL ≥56 mm; Pérez i de Lanuza et al. 2013), about half of them show autotomized/regenerated tails. Frequencies are calculated by pooling males and females. *White numbers at the bottom of the bars* indicate the sample size by range of SVL

(i.e. detection by eavesdroppers). Contrary to expectations, our results show no evidence of behavioural compensation for differences in conspicuousness in colour morphs, at least with respect to the adoption of different postures. Our results also argue against an alternative scenario in which the most conspicuous morphs increase their signal efficacy adopting postures that maximize their intrinsic detectability, exaggerating the differences in conspicuousness between colour morphs.

The idea that animals may evolve compensatory traits in response to the negative effects of sexually selected traits has received some empirical support. Compensatory traits have been described in several taxa, but more information is needed to assess the generality of compensation for ornamental traits, particularly in terrestrial animals (Husak and Lailvaux 2014). Results for birds are somewhat controversial. Birds with conspicuous colorations respond more to acoustic signals of predators (Journey et al. 2013) but do not compensate for their greater visual conspicuousness by fleeing sooner from approaching threats (Hensley et al. 2015). Our results show no compensatory behaviours for lizards in the exposure of their conspicuous colour patches. However, colour morphs could still differ in other characteristics, such as activity patterns, antipredator behaviour (e.g. boldness) or microhabitat use (Carretero et al. 2006), undetected in the present study, that might affect the trade-off between signal detection and vulnerability to eavesdroppers. Additionally, achromatic conspicuousness may be more important for prey detection than we assumed here and interact with or override the effect of chromatic conspicuousness.

The apparent lack of compensatory behaviours between morphs could be taken as an indication that the differences in detectability to predators have negligible fitness consequences, especially given that the conspicuous colorations are located ventrally. For ventral coloration, viewing angle may strongly affect visibility and conspicuousness in natural

Table 4 Results of log-linear models including the five alternative colour morphs

	χ^2	*df*	*P* value
K-factor interactions			
Sex	223.94	6	<0.00001
Morph	34.41	9	<0.0001
Tail loss	8.87	4	0.06
Partial association			
Sex	42.22	1	<0.00001
Morph	82.75	4	<0.00001
Tail loss	53.14	1	<0.00001
Sex × morph	19.70	4	0.0005
Sex × tail loss	3.19	1	0.074
Morph × tail loss	8.59	4	0.072
Marginal association			
Sex × morph	21.04	4	0.0003
Sex × tail loss	4.52	1	0.031
Morph × tail loss	9.92	4	0.042

Results excluding the two rare intermediate morphs are identical

Table 3 Number of observed females and males showing regenerated or original tails and the percentage of regenerated tails classified by morph in our sample

	White	Yellow	Orange	White-orange	Yellow-orange
Females					
N regenerated tail	21	38	18	17	22
N original tail	25	19	7	15	10
% Regenerated tails	46	67	72	53	69
Males					
N regenerated tail	79	69	54	15	18
N original tail	35	27	16	9	19
% Regenerated tails	69	72	77	63	49

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circumstances. However, our approach to the damaging costs of conspicuousness using the frequencies of tail loss provides indirect confirmation that morphs indeed incur different predation risk and/or social costs. Considering only the three pure morphs, the more chromatically conspicuous morphs (i.e. yellow and orange) show the highest frequency of tail loss. The frequency of tail loss is only a crude estimate of predation risk because the incidence of autotomy may indicate exposure to inefficient predation (Medel et al. 1988), and tail losses can also be caused by social interactions (Lazić et al. 2012). Moreover, tail loss is strongly influenced by age (i.e. older lizards have a higher probability to have regenerated tails than younger lizards; in our population, 45 % of tail losses occur before lizards completely develop their ventral coloration, i.e. SVL <56 mm; see Fig.4). However, as body size is directly correlated with age in species with indeterminate growth (Caetano et al. 1986) and morphs differ only slightly in body size (Pérez i de Lanuza et al. 2013), it is unlikely that the differences in tail loss among morphs are a by-product of body size. Instead, they suggest that the different morphs experience different predation pressure possibly due, at least in part, to differences in their conspicuousness. Alternatively, the different frequencies of tail loss may reflect morph-specific differences in the efficacy of predator avoidance or in other aspects of behaviour that expose lizards to predators (e.g. patrolling, courtship, fights).

Our results highlight the relevance of lizard temperature and thermal environment for the display of the conspicuous colour patches. In our analyses, body temperature emerged as the only variable strongly and positively correlated with lizard posture. Lizards with high body temperature tend to display more their conspicuous coloration than lizards with lower body temperature. The correlation between body temperature and posture agrees with data from other lizard species (e.g. Muth 1977) and has traditionally been interpreted in the context of behavioural thermoregulation, especially in desert ground-dwelling lizard species. Raised body postures are often considered a means to avoid contact with dangerously hot substrates and to radiate excess heat. However, our results do not support this interpretation because we did not find differences in substrate temperatures between lizards adopting postures 2, 3 and 4, suggesting that thermoregulation alone cannot explain why lizards adopt elevated postures (i.e. 3 and, especially, 4).

Our results suggest a more complex scenario encompassing thermoregulation, predator avoidance and signalling behaviour. Based on the well-known relationship between body temperature and antipredator behaviour (Rand 1964; Hertz et al. 1982; Huey 1982), we suggest that lizards adopt elevated postures only when they attain a body temperature high enough for an efficient escape response. At low body temperatures, when locomotor performance is likely to be suboptimal and lizards have reduced chances of escaping from a predator (Bauwens et al. 1995), they adopt low postures that conceal their conspicuous colour patches increasing the probability of remain undetected. Only after they warm up and reach high body temperatures can lizards afford the increased predation risk incurred by making themselves more visible to predators. This alternative explanation emphasizes the intricate network of evolutionary and ecological factors that are likely to shape lizard behaviour and suggests that selection pressures related to communication deserve more attention than they have so far received in studies of lizard thermoregulation and antipredator behaviour.

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Compliance with ethical standards An attempt was made to minimize lizard disturbance during observations. At worst, lizards avoided the observer by moving away. No lizards were captured or manipulated during the observations. The habitat (i.e. rocks, vegetation) was not altered in any way. Field work was performed under research permit number 2013095-0001 issued by the Préfecture des Pyrénées-Orientales (France). This research complied with the ASAB/ABS Guidelines for the Use of Animals in Research.

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