Ecology and Evolution

Conspicuous male coloration impairs survival against avian predators in Aegean wall lizards, *Podarcis erhardii*

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Abstract

Animal coloration is strikingly diverse in nature. Within-species color variation can arise through local adaptation for camouflage, sexual dimorphism and conspicuous sexual signals, which often have conflicting effects on survival. Here, we tested whether color variation between two island populations of Aegean wall lizards (*Podarcis erhardii*) is due to sexual dimorphism and differential survival of individuals varying in appearance. On both islands, we measured attack rates by wild avian predators on clay models matching the coloration of real male and female *P. erhardii* from each island population, modeled to avian predator vision. Avian predator attack rates differed among model treatments, although only on one island. Male-colored models, which were more conspicuous against their experimental backgrounds to avian predators, were accordingly detected and attacked more frequently by birds than less conspicuous female-colored models. This suggests that female coloration has evolved primarily under selection for camouflage, whereas sexually competing males exhibit costly conspicuous coloration. Unexpectedly, there was no difference in avian attack frequency between local and non-local model types. This may have arisen if the models did not resemble lizard coloration with sufficient precision, or if real lizards behaviorally choose backgrounds that improve camouflage. Overall, these results show that sexually dimorphic coloration can affect the risk of predator attacks, indicating that color variation within a species can be caused by interactions between natural and sexual selection. However, more work is needed to determine how these findings depend on the island environment that each population inhabits.

Introduction

Intraspecific color divergence has attracted much scientific interest as a model system to study evolution. Across a range of animals, divergence arises through sexual dichromatism, whereby selection typically favors conspicuous signals in males for mating and sexual competition, while camouflage against predators is generally more important in females (e.g., Andersson 1994; LeBas and Marshall 2000; Alonso-Alvarez et al. 2004; Stuart-Fox et al. 2004; Cummings et al. 2008; Gomez et al. 2009; Bajer et al. 2010, 2011; Higham et al. 2010; Pérez i de Lanuza et al. 2013; Marshall and Stevens 2014). However, conspicuous

signals in males may increase the risk of detection and attack by predators (e.g,. Godin and McDonough 2002; Macedonia et al. 2002; Kwiatkowski and Guyer 2003; Stuart-Fox et al. 2003; Husak et al. 2006; but see Götmark 1992, 1993), especially when predators have visual systems tuned to detect the communication signals of their prey (e.g., Ryan et al. 1982; reviewed by Zuk and Kolluru 1998; Stevens 2013). Nevertheless, increasing evidence shows that certain adaptations can offset the potential costs of conspicuous coloration, such as signal partitioning and private channels of communication to reduce detection by eavesdroppers (e.g., Cummings et al. 2003; Siebeck 2004; Stuart-Fox et al. 2004; Håstad et al. 2005; Cummings et al. 2008;

Oliver et al. 2009; Gluckman and Cardoso 2010; Clark et al. 2011; Garcia et al. 2013; Marshall and Stevens 2014; reviewed in Brandley et al. 2013; Stevens 2013).

In addition to sexual dimorphism, classic work has shown that color divergence can be caused by adaptation to local environments to optimize camouflage and sexual signaling (Endler 1978, 1980). More recent advances have demonstrated that, under certain conditions, distinct local environments driving intraspecific diversification in camouflage and sexual signals can lead to reproductive isolation among populations (reviewed in Boughman 2002; Schluter 2009; Stevens 2013).

Although many studies assume that conspicuous coloration is costly to survival, surprisingly few have directly tested whether it does increase the risk of attack from predators across varying local environments, instead relying on measurements of relative degrees of matching against different backgrounds (e.g., Rosenblum et al. 2004; Stuart-Fox et al. 2004; Hoekstra et al. 2005; Rosenblum 2006; Rosenblum et al. 2010; Marshall and Stevens 2014; McLean et al. 2014; but see for example Vignieri et al. 2010). However, it is important to understand whether conspicuous coloration directly increases the risk of predator detection and attack because this corroborates why selection should favor enhanced local camouflage and adaptations that resolve conflict between camouflage and conspicuous signals.

An established and effective way to test the impact of conspicuousness on predator detection has been to measure attack rates by wild predators on artificial models resembling prey coloration, as a proxy for survival of real animals (e.g., Stuart-Fox et al. 2003; Vignieri et al. 2010; Valkonen et al. 2011). Such survival experiments have supported the prediction that conspicuous color patterns increase the risk of attack by avian predators and that attack risk increases in non-local environments where coloration has not adapted to match backgrounds for camouflage (e.g., Stuart-Fox et al. 2003; Husak et al. 2006; Stobbe and Schaefer 2008; Vignieri et al. 2010; Farallo and Forstner 2012).

However, the above experiments rarely consider the visual capabilities of avian predators, either in the design of the models to replicate prey coloration or in determining how conspicuous the models are against the background to predators, even though hunting birds have different visual systems to humans (for instance, they can see ultraviolet light and probably a greater range of colors; Hart 2002; Lind et al. 2013). Therefore, in survival experiments, it is important to closely imitate prey coloration and conspicuousness against natural local backgrounds with regard to avian vision (e.g., Stuart-Fox et al. 2003). Such methods are more likely to accurately determine how predation influences the differential evolution of coloration across varying local environments.

Island populations of Aegean wall lizards (*Podarcis erhardii*) are a valuable system for this type of study because they show color variation among their distinct environments that enhances local camouflage against avian predators (Marshall and Stevens 2014; Marshall et al., in press). Specifically, while sexually competing males are more conspicuous than females, selection has favored relatively cryptic coloration on exposed dorsal regions, presumably to counteract the increased likelihood of detection by aerially hunting avian predators, and this may vary depending on local island ecology (e.g., degree of predation risk; Marshall and Stevens 2014). Moreover, both sexes match their local background environment for camouflage against birds, as similarly shown in other lizards and mice (e.g., Rosenblum et al. 2004; Stuart-Fox et al. 2004; Rosenblum 2006; Vignieri et al. 2010; McLean et al. 2014; Marshall et al., in press). However, it is unknown whether coloration in *P. erhardii* directly decreases detection and subsequent attack by eavesdropping avian predators in local environments.

In this study, we performed an experiment to test the influence of *P. erhardii* coloration on survival. We measured attack rates on artificial models of *P. erhardi* designed to replicate the actual dorsal coloration of males and females from two island populations, as perceived by avian predators. We predicted that (1) models exhibiting more conspicuous male coloration were more likely to be attacked by avian predators than less conspicuous female-colored models, and (2) avian attacks on models were less likely to occur in local island environments than in non-local environments due to enhanced local camouflage.

Materials and Methods

Study species and sites

The Aegean wall lizard (*Podarcis erhardii;* Bedriaga 1882) is a diurnal, small lacertid widespread throughout many Aegean islands where it is found in all island ecosystems (Valakos 1986; Arnold and Ovenden 2002). It is listed as a species of "Least Concern" under the IUCN Red List classification for species at risk of global extinction (Cox and Temple, 2009*)*. Field research and experiments were conducted with permission from the Greek Ministry of Environment (research permit number: 166648/356). Photographic color sampling of *P. erhardii* was conducted during April–May and August 2012 and survival experiments with clay models were carried out in June and in August 2013 on two Aegean islands, respectively: Syros (37°27′N, 24°54′E) in the Cyclades island group and Skopelos (39°7′N, 23°43′ E) in the northern Sporades island group. The land used for fieldwork was publicly accessible.

In situ photographic sampling of *Podarcis erhardii* coloration

We followed the general photographic sampling, image analysis, and visual modeling methods described in Marshall and Stevens (2014). We used digital imaging to obtain color samples of free-ranging lizards (see Stevens et al. 2007; Marshall and Stevens 2014). We took images of stationary lizards and their corresponding backgrounds with a Fujifilm IS Pro ultraviolet (UV)-sensitive digital camera with a quartz CoastalOpt UV lens (Coastal Optical Systems), fitted with a UV and infrared (IR) blocking filter for photographs in the human-visible spectrum (Baader UV/IR Cut filter; transmitting between 400 and 700 nm), and with a UV pass filter (Baader U filter; transmitting between 300 and 400 nm) for UV images. After the photographed lizard had fled, we took human-visible and UV images of a Spectralon™ grey reflectance standard (Labsphere, Congleton, UK), which reflects light equally at 40% between 300 and 750 nm, to standardize photographs for ambient light conditions (the "sequential method"; see Bergman and Beehner 2008; Stevens et al. 2009).

We recorded photographed lizards' locations using a Garmin eTrex® GPS device (Schauffhausen, Switzerland) and marked them with colored tape to indicate sex and lifestage estimated using a field guide (Arnold and Ovenden 2002). We confirmed these estimations were 99% reliable by comparing estimated (from photographs) and observed sex and lifestages from captured lizards (see Marshall and Stevens 2014). We avoided pseudoreplication by never repeating photography of a lizard of the same sex within the same home range (i.e., within 10 m) (Verwaijen and Van Damme 2008).

Image analysis and visual modeling

Human-visible and UV images of lizards and their backgrounds were linearized with respect to light intensity (Stevens et al. 2007) and transformed to reflectance (RGB-equalized) to remove any effects of different light conditions (see Stevens et al. 2007; Troscianko and Stevens 2015). Any images that were overexposed and/or could not be RGB-equalized were discarded from the analysis.

We then transformed our images to correspond to avian predicted photon catch cone values using a mapping process (see Stevens et al. 2007; Pike 2011; Troscianko and Stevens 2015). We used the calculated spectral sensitivity of our camera's sensors to convert the aligned images from camera color space to the relative photon catches of avian longwave (LW), mediumwave (MW), shortwave (SW), and UV-sensitive cone (color) photoreceptors and double cone (luminance) photoreceptors using the spectral sensitivity of a peafowl (*Pavo cristatus*; Hart 2002) and of a blue tit (*Parus caeruleus;* Hart et al. 2000). The peafowl visual system is often used as a representative of the violet-sensitive (VS) class of color vision in birds (Cuthill 2006; Hart and Hunt 2007), which is typical of raptors and corvids that are major visual predators of adult lizards in Europe (Handrinos and Akriotis 1997; Castilla et al. 1999), whereas the blue tit visual system is often used as a model of the ultraviolet-sensitive (UVS) class of color vision in birds (e.g., Hart et al. 2000; Cuthill 2006; Stoddard and Stevens 2011). Raptors (buzzards and falcons e.g. *Buteo buteo, Falco tinnunculus, Falco eleonorae*) and corvids (e.g. hooded crows, *Corvus cornix*) are the most prevalent avian predator in our study sites (personal observations) and thus birds with VS vision are likely to be the most important type of avian predator (Ödeen and Hastad 2013). However, we considered that other birds with UVS color vision present in our study sites are known to prey on lizards (e.g., gulls and some Turdidae species; Castilla and Labra 1997; Handrinos and Akriotis 1997; Collar 2005; Sazima and D'Angelo 2011; Ödeen and Håstad 2013). Therefore, we used both VS and UVS avian models to account for any predation attempts by birds with either type of color vision, although we treat VS raptors and corvids as the more important types of avian predators. The calibrations were performed in MATLAB v. R2011b (The MathWorks, Inc., Natick, MA) using custom-written programs. Calibrations were restricted to the 300–700 nm range, which encompasses most of the visual spectrum of diurnal birds (Hart and Hunt 2007).

LW, MW, SW, and UV photon catches of lizards were extracted from the calibrated images in ImageJ using the selection tool and a purpose-written script. Lizard selections were made from anterior and posterior dorsal areas due to observed color differences between these regions. Selection criteria were standardized across all images: anterior selections were taken next to the base of the tail and posterior selections were taken next to the base of the head. We calculated the average photon catch between lizards' anterior and posterior regions to yield an overall mean for the dorsal surface of Syros male and female lizards and of Skopelos male and female lizards.

Model design

Models were designed to resemble the size and shape of *P. erhardii*. We made 3-D molds of a preserved adult specimen of a closely related species, the common wall lizard (*Podarcis muralis*), captured in Dorset, UK (R. Heathcote, 2011, pers. comm). Molds were created using

Gedeo "Siligum" molding paste (Pébéo, Gémenos, Provence, France) to create identical casts made of a mixture of FIMO® soft polymer clay (Staedtler, Bridgend, Wales) and Sculpey® III polymer clay (Polyform Products Company, Elk Grove Village, IL). We used this clay mixture because it does not harden in high temperatures to ensure predator attack marks could be seen in the clay.

Models were designed to resemble the dorsal color and luminance of Syros and Skopelos male and female *P. erhardii* as modeled to avian vision. Specifically, because anterior and posterior dorsal coloration of *P. erhardii* can

vary (Fig. 1; Marshall and Stevens 2014), we designed the models so that the clay colors matched, as closely as possible, an average avian photon catch of the anterior and posterior dorsal regions in both male and female lizards from each island population (derived from image analysis and visual modeling, as described above). Although imperfect, we used the average dorsal coloration as our lizard color reference for two reasons. First, because *P. erhardii* dorsal coloration can be extremely variable, even within the same sex (see Fig. 1), so that achieving accurate replicas of all types of dorsal coloration would be
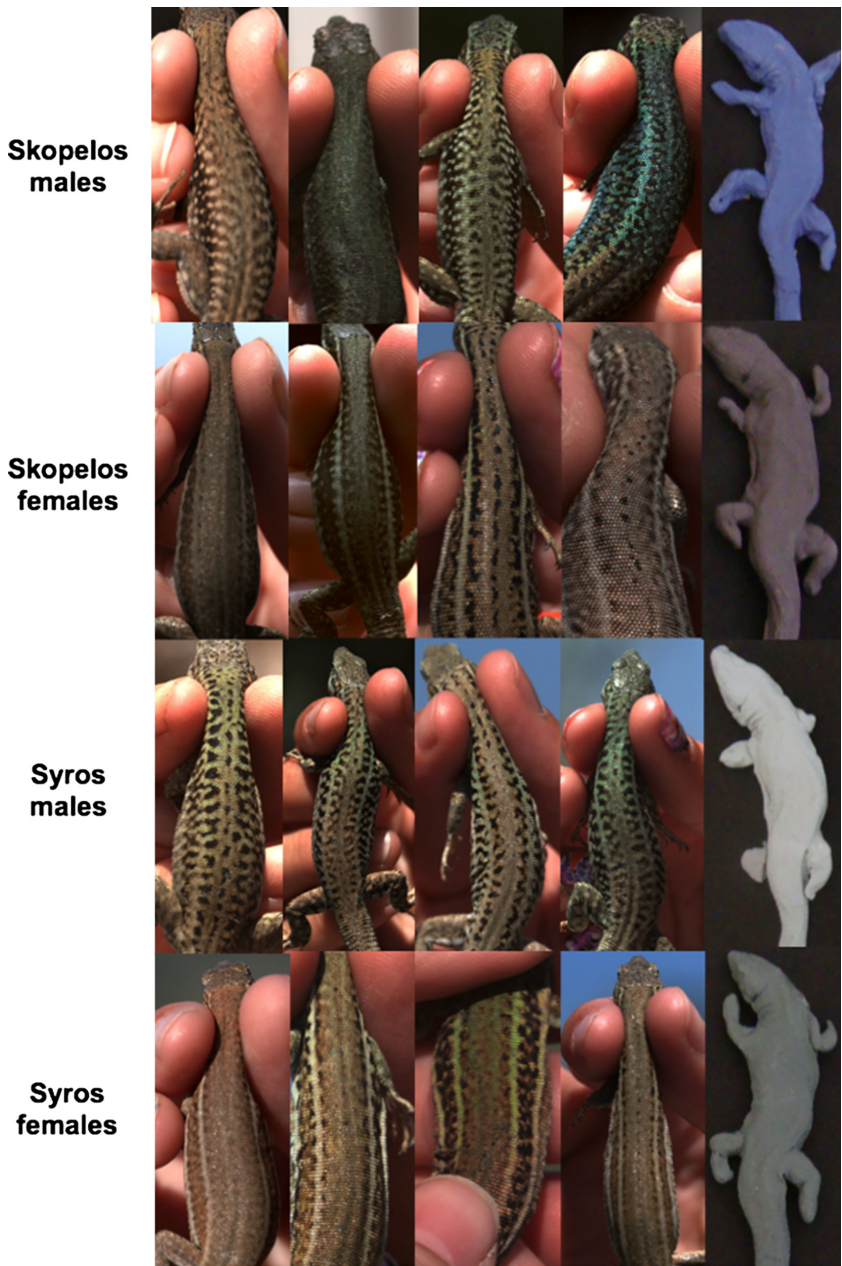

Figure 1. Example images of Aegean wall lizards (*Podarcis erhardii*) and equivalent model replicas. Male and female *P. erhardii* from the focal Skopelos and Syros populations are shown alongside the models that were designed to resemble their size, shape, color, and brightness (luminance). Note that the models are calibrated to violet-sensitive (VS) avian predator color vision, whereas images of lizards are perceived by the human visual system.

very difficult. Second, we aimed to design models so that they resembled the coloration of all dorsal regions potentially viewed by aerial predators. An average coloration of the anterior and posterior regions facilitated this given the difficulty of finding clay colors that closely matched avian-perceived lizard coloration (see below). We acknowledge, however, that at relatively close range, different parts of lizards' backs may not have the same detection probabilities.

We used reflectance spectrometry to measure potential clay colors as a complementary method to the image analysis methods described above. We used spectrometry in the laboratory to measure multiple point samples of clay, so that we could quickly inspect potentially useful clay colors by looking at their reflectance spectra. Although digital imaging would also be appropriate for this type of analysis, its primary use is in sampling live animals in the field (i.e., under natural light conditions; see Stevens et al. 2007). We obtained reflectance spectra of different clay color samples using an Ocean Optics USB2000 + spectrophotometer (Dunedin, FL) with illumination by a PX-2 pulsed Xenon lamp. We used a narrow-ended (1/8″) probe held at a constant distance and a 45° angle to the clay surface and measured reflectance at 1-nm intervals from 300 to 700 nm, expressed relative to a Spectralon™ 99% white reflectance standard (Labsphere). As there was negligible variation in reflectance spectra of each clay color sample, we took one measurement per sample. Reflectance spectra were transformed to peafowl and blue tit cone photon catches (Hart et al. 2000; Hart 2002) in MATLAB using a custom-written program. Calibrations were restricted to 300–700 nm (Hart and Hunt 2007).

To determine how effectively the clay colors matched the average dorsal coloration of male and female *P. erhardii*, as perceived by avian predators, we quantified chromatic and achromatic contrast between lizard photon catches (obtained from image analysis of Syros and Skopelos lizards as described above) and model (clay) photon catches (transformed from reflectance spectra).

We quantified color and luminance contrast between real lizard and model photon catches according to the log form of the Vorobyev and Osorio (1998) receptor noise model. We used a Weber fraction value of 0.05 for the most frequent cone type based on data in other vertebrates (Vorobyev and Osorio 1998; Vorobyev et al. 1998) and relative proportions of color cone types in the retina for peafowl (*P. cristatus*) (LW = 0.92, MW = 1.00, SW = 0.81, UV = 0.54; Hart 2002) and for blue tits (*P. caeruleus*) (LW = 1.00, MW = 0.99, SW = 0.71, UV = 0.37; Hart et al. 2000). The results of these models are expressed in "just noticeable differences" (JND). Generally, a JND of less than 1.00 indicates that two stimuli are indistinguishable; values between 1.00 and 3.00 should be difficult to discriminate except under controlled, optimal light conditions; and values increasing above 3.00 indicate increasingly better discrimination (Siddiqi et al. 2004). Therefore, we aimed to find the best possible match (approximately 3.00 JND or below) between our experimental models and actual lizard coloration.

Calibrations of clay model coloration to match actual lizard coloration

We used an iterative approach to find clay color and luminance that matched actual lizard color and luminance, by testing approximately 300 different clay colors that comprised various mixtures of different FIMO and Sculpey III colors. We found four clay colors that met our criteria for the four experimental treatments by approximately matching (i.e., ≤3.00 JND) actual Syros and Skopelos male and female *P. erhardii* average dorsal color and luminance, as perceived by birds with UVS and VS color vision (see Table 1). For the control treatment, we chose a brown color that did not match actual lizard coloration and luminance (>3.00 JND) and was not brightly colored so as to avoid startling predators (see Table 2). As the clay colors involved mixing different colors and amounts of colors together, we ensured that each batch of clay color was mixed in precisely the same way

Table 1. Degree of contrast between real lizards versus experimental models (JND). Showing "just noticeable differences" (JND) between the experimental clay model treatments and the coloration of real male and female *P. erhardii* from Syros and Skopelos island populations, with regard to a model of violet-sensitive (VS) avian predator color vision (*Pavo cristatus*) and a model of ultraviolet-sensitive (UVS) avian color vision (*Parus caeruleus*), and to a model of luminance (double cone) vision for both. Values approximately ≤3.00 JND depict models that are generally indistinguishable from actual lizards by birds in terms of color and luminance.

| Real lizards versus experimental models (JND) | VS vision | | | | UVS vision | | | |
| | Syros | | Skopelos | | Syros | | Skopelos | |
	Female	Male	Female	Male	Female	Male	Female	Male
Color	3.01	3.52	2.80	3.69	2.75	3.26	2.69	3.56
Luminance	0.22	0.45	0.84	0.64	0.22	0.45	0.84	0.64

Table 2. Degree of contrast between real lizards versus unmatched control model treatment (JND). Showing "just noticeable differences" (JND) between the control model treatment and the coloration of real male and female *P. erhardii* from Syros and Skopelos island populations, with regard to a model of violet-sensitive (VS) avian predator color vision (*Pavo cristatus*) and a model of ultraviolet-sensitive (UVS) avian color vision (*Parus caeruleus*), and to a model of luminance (double cone) vision for both. Generally, >3.00 JNDs show that the control treatment is distinguishable (unmatched) from actual lizards by predatory birds, in terms of color and luminance contrast.

Real lizards versus control model (JND)	VS vision				UVS vision			
	Syros		Skopelos		Syros		Skopelos	
	Female	Male	Female	Male	Female	Male	Female	Male
Color	16.05	18.67	20.00	22.66	14.77	17.6	18.47	20.99
Luminance	42.52	47.04	35.13	37.10	42.52	47.04	35.13	37.10

and tests of variation between different batches revealed little variation in reflectance spectra.

Crucially, the JND analysis confirmed that half of the models matched avian-perceived (average) dorsal coloration of the lizards they were designed to resemble (i.e., ≤3.00 JND) and the other treatments were very close to 3.00 JND (i.e., no higher than 3.69 JND; Table 1). Moreover, all of the model treatments were extremely close luminance matches to the real lizards (i.e., <1.00 JND; Table 1). In addition, to illustrate how closely matching the different model treatments were to that of real lizard coloration from each island population, we plotted avian predator (VS peafowl) photon catches of the models derived from reflectance spectra and of the real lizards obtained from image analysis in tetrahedral color space (see Endler and Mielke 2005; Fig. 2).

Survival experiments

On each of the two focal islands (Syros and Skopelos), models were placed along ten non-linear 300-m transects. Each transect was located in different remote areas which were at least 1 km apart, not adjacent to each other, and naturally inhabited by *P. erhardii*. Each transect consisted of 30 models (six of each of the five treatments) placed at 10-m intervals, totaling 300 models tested on each island (600 models overall). We used transects in different areas and at widely spaced intervals to minimize the number of models that the same individual predator might encounter. Treatment order along transects was the same for each transect (i.e., in a preplanned order) to prevent experimenter bias when placing models on backgrounds and to ensure that a predator would potentially encounter any one of the five treatments in a given area. The first and final model on each transect was recorded on the GPS device for subsequent checks for predator attacks. The models were placed at approximately the same height off the ground in open environments on rocks in remote rural locations. This imitated where real lizards usually bask and where they are potentially visible to avian predators (e.g., Bauwens et al. 1996) and was comparable to previous measurements of *P. erhardii* camouflage against rock backgrounds (Marshall and Stevens 2014; Marshall et al., in press).

We checked all models at 24-, 48-, 72-, 96-, and 120-h intervals and noted any signs of predator attacks. Models with attack marks on them were noted as attacked, removed, and not replaced to minimize how many models were encountered by the same predator, as is typical in this type of experiment (e.g., Cuthill et al. 2005; Stevens et al. 2006; Stobbe and Schaefer 2008; Farallo and Forstner 2012). We classified models that exhibited unambiguous clear triangular beak/stab marks together with obvious signs of attack (flipped over, in pieces and/or moved) as attacked by avian predators (see Fig. 3). For instance, some models were found with beak/stab marks on the head, often so that the head was separated from the body, and one model's head was found 10 m away in a nearby field. Occasionally, we found models that had been pecked all over were in pieces and/or overturned and far away from the original location. When checking the models, we noted where on the model avian attack marks were found. These were classified into three locations of attack: (1) only head, (2) only body (including body, legs, and tail), and (3) both head and body. Models that had heads missing or that were separated from the body were classified as attacked on the head if no other body part showed attack marks. Models with small teeth marks or any other marks were classified as attacked by non-avian predators (e.g., snakes, rodents, and insects) (see Fig. 3). We recorded models with no marks after 120-h as not attacked. We classified any models that could not be found as missing, although the possibility that a bird had seized and flown off with them was considered in the analysis. Specifically, we performed two survival analyses: (1) with the missing models treated as unattacked (censored) and (2) with missing models classified as attacked. We qualitatively compared the results of the two analyses to determine any differences

due to missing models being classified as attacked or unattacked.

Conspicuousness of clay models against experimental backgrounds

To confirm differences in how conspicuous the different model color treatments were to avian predators, once the experiments had finished, we took human-visible and UV images of a proportion of randomly selected models on each island ($N = 108$; 18% of the 600 models) against their experimental backgrounds. Models were selected for photography using a randomly generated number table. We followed the general methods described above for photography, image analysis, and visual modeling, with some differences. We included the reflectance standard in the same images for subsequent image analysis in ImageJ, in which only one selection was made of the dorsal surface, due to the uniformity of model coloration. Moreover, we selected one rock
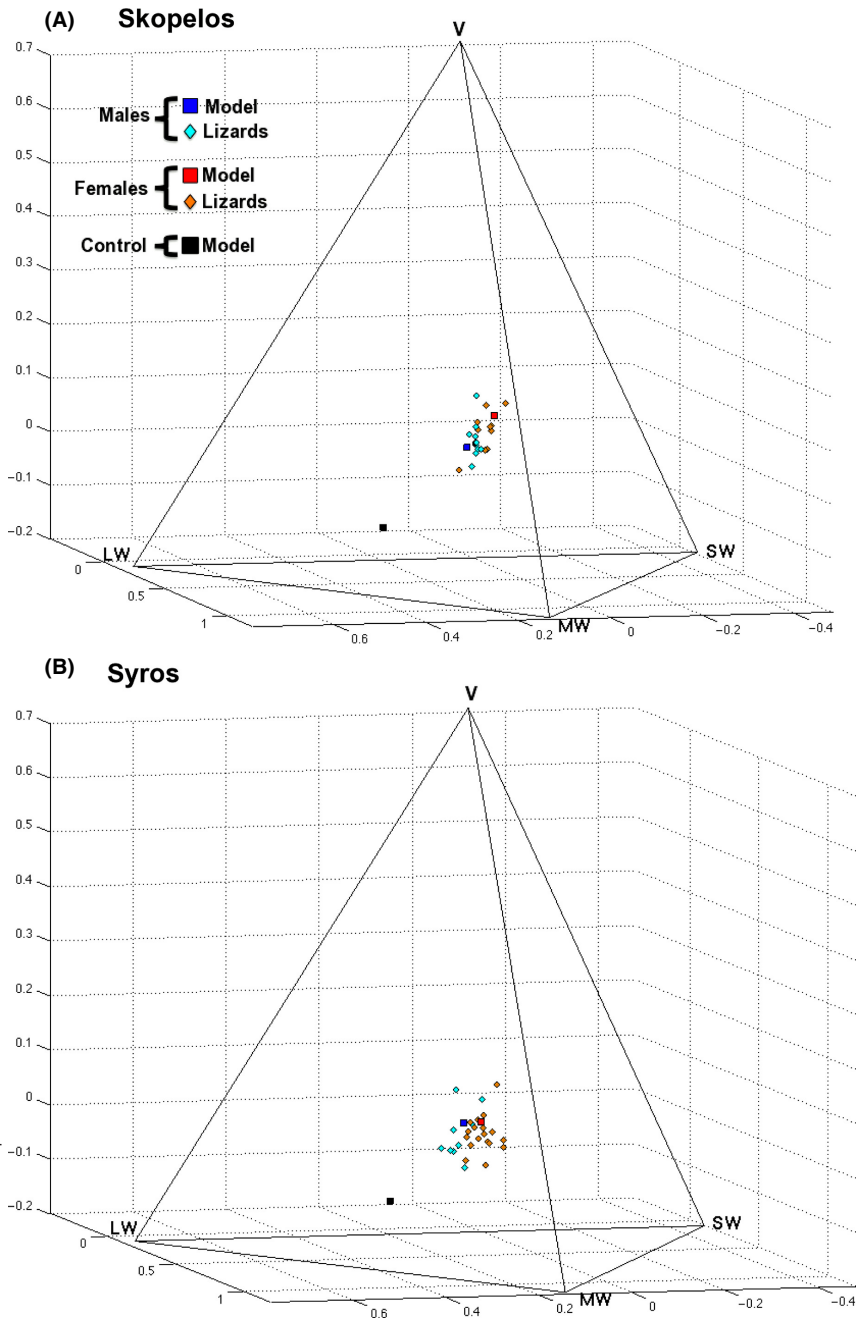

Figure 2. Distributions of coloration of Aegean wall lizards *(Podarcis erhardii)* and replicate clay models in tetrahedral (avian predator) color space. Each color is a point in the tetrahedron determined by the relative stimulation of the four color cone channels (v, sw, mw and lw) of a typical violet-sensitive avian predator visual system (peafowl; *Pavo cristatus*). In each focal island population (A: Skopelos and B: Syros), data points depict male- and female-colored models (blue and red squares), which were designed to resemble avian-perceived male and female *P. erhardii* coloration (light blue and orange diamonds), and an unmatched control model (black square).
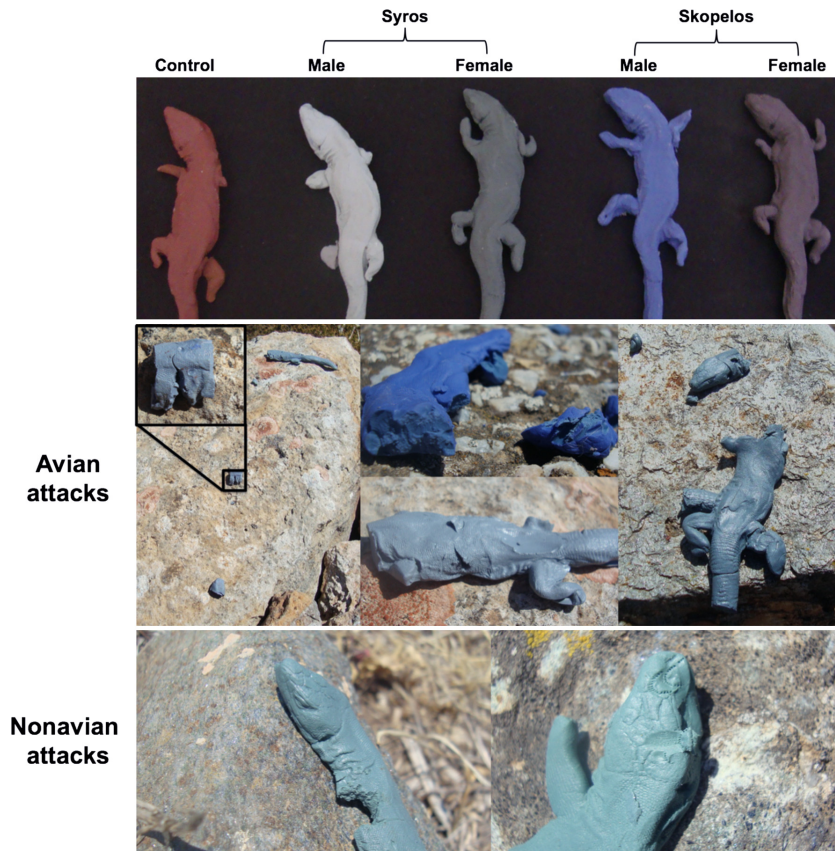
Figure 3. Above: The five model treatments used in the survival experiments (left to right): brown control (unmatched to real lizard coloration), Syros male, Syros female, Skopelos male, and Skopelos female. Below: examples of avian and non-avian attacks on models.

background area in each calibrated image, which was based on the same criteria described above. Through these selections, we obtained avian predator (VS) photon catches of models and their corresponding backgrounds, which were compared using the Vorobyev and Osorio (1998) receptor noise model to generate color and luminance JNDs.

Predictions and statistical analyses

Verification of model design

Our first objective was to test our assumptions regarding the design of the models. First, we aimed to verify that the models occupied similar areas of avian (tetrahedral) color space to that of the real lizards they were designed to resemble. Second, we aimed to confirm whether avian attacks were directed at the head more frequently than on other body parts, to indicate that the predators recognized the models as prey. Lastly, we aimed to ascertain that non-local and male models were more conspicuous to avian predators than local and female models on each experimental island by conducting the following statistical analysis. The models versus background (JND) data were

not normally distributed, with a substantially positively skewed distribution, so we transformed this data to normality using a logarithmic transformation, although we report raw (back-transformed) data in figures and quoted mean $\pm$ SE values.

We used the transformed JND data in a multivariate general linear model (GLM) with experimental island (Syros vs. Skopelos), model locality (non-local vs. local), and model sex (male vs. female) as between-subjects factors and tested for two-way factor interactions to determine whether each factor had independent effects on model conspicuousness. We report the size of the effects in partial ETA^2 (η_p^2), which can be interpreted as the proportion of variance in the dependent variable that is attributable to each effect. Planned comparisons were conducted by rerunning the GLM with only the variables that were relevant to our predictions, ensuring that the number of comparisons did not exceed spare experimental degrees of freedom (*n*-1), because this method is more powerful than using conservative multiple post hoc tests (Ruxton and Beauchamp 2008). Any interactions that were nonsignificant were removed from the analysis, and the model was rerun without them.

Model survival

We then addressed whether the model treatments identified as being different in conspicuousness were attacked at different rates by wild predators, as a measure of survival. We predicted that non-avian predators (e.g., rodents, snakes) would attack models irrespective of their visual conspicuousness because they also use olfactory and other cues to hunt (e.g., Buning 1983; Vander Wall et al. 2003; Hughes et al. 2010). In contrast, we predicted that visually oriented hunting birds, which are major predators of small lizards (e.g., Handrinos and Akriotis 1997; Castilla et al. 1999), would attack models that were more conspicuous (non-local and male) more frequently than models that were less conspicuous (local and female).

To test these predictions, we conducted a separate Cox regression survival analysis for each island (Syros and Skopelos) using an Enter method with model color treatment (Syros male, Syros female, Skopelos male, Skopelos female, and control) and experimental study site (transect block) included as categorical covariates. Unattacked models were categorized as censored in the analysis. We conducted two analyses per island: the first included all attacks (non-avian and avian) and the second included only likely avian attacks, with models that were missing classified as censored. All analyses were carried out again with missing models classified as "attacked" to account for the possibility that birds had seized and flown away with them. Planned pairwise tests were conducted by rerunning the Cox regression analyses on only data relevant to test our predictions. Again, we undertook a number of planned comparisons that did not exceed spare degrees of freedom (*n*-1) (Ruxton and Beauchamp 2008).

Results

Verification of model design

Tetrahedral color plots illustrate that avian predator (VS system) cone stimulation by real *P. erhardii* coloration occupied similar areas of color space to that of the replicate models we designed (Fig. 2). Specifically, avian cone stimulation by real male and female coloration showed a clustered distribution around the corresponding male and female model treatments for each island (Fig. 2). Female *P. erhardii* appeared more shifted toward the sw/mw region compared to males, and accordingly the female- and male-colored models showed a shift toward their equivalent regions. Moreover, the control (unmatched) model treatment occupied a different region of color space to that of the real lizard coloration (shifted more toward the lw/mw region; Fig. 2). These plots indicate that we met the experimental criteria for our model

design. That is, avian predators should perceive the four experimental model treatments as similar to that of real *P. erhardii* coloration, and also that the control treatment was unmatched, as confirmed by our a priori analyses testing how well models matched the real lizards (JND; see Tables 1 and 2).

Avian attack location on the models

On both islands, the large majority of avian attacks on the models were found on the head region, either as a single attack to the head or as an attack to both the head and other body region (i.e., body, legs or tail) (Skopelos = 97% of attacks, Syros = 82%; Table 3). On Skopelos, attacks on both the head and other body regions represented the largest proportion of attacks (61%), while on Syros, single attacks on the head were equally as frequent as attacks to both head and other body parts (41%). On both islands, attacks directed at only the head were more frequent than attacks directed only at other body regions (Table 3).

Conspicuousness of model treatments

The GLM reported that there were highly significant effects of island (i.e., which island the experiment was conducted on) and model sex treatment on the chromatic conspicuousness of the models (sex: $F_{1,100} = 37.398$, $P < 0.001$, $\eta_p^2 = 0.272$; island: $F_{1,100} = 11.324$, $P = 0.001$, $\eta_p^2 = 0.102$). Moreover, there were significant interactions between island and model locality (i.e., whether the models were designed to be "local" or "non-local" in color; $F_{1,100} = 55.192$, $P < 0.001$, $\eta_p^2 = 0.356$) and between island and model sex ($F_{1,100} = 5.056$, $P = 0.027$, $\eta_p^2 = 0.048$). There were no other significant factor interactions, and there were no significant factor effects on luminance (achromatic) conspicuousness of the models. These results are interpreted below from planned comparisons.

Male versus female conspicuousness

We verified that, on both islands, we achieved our planned model design to produce male models that were more conspicuous than female models (although only in terms of

Table 3. Location of avian attack marks on models. Number and proportion of models showing avian attack marks on both the head and other body regions (i.e., body, legs, and tail), and on only the head or only on other body regions.

Island	Number of avian attacks on models and attack region			
	Total	Head and body	Only head	Only body
Skopelos	31	19 (61%)	11 (36%)	1 (3%)
Syros	22	9 (41%)	9 (41%)	4 (18%)

chromatic contrast) and this effect was more evident on Skopelos than on Syros (Fig. 4; Skopelos: $F_{1,64} = 21.763$, $P < 0.001$, $\eta_p^2 = 0.254$; Syros: $F_{1,40} = 5.514$, $P = 0.024$, $\eta_p^2 = 0.121$; Skopelos males = [mean ± SE JND] 11.154 ± 0.886, Skopelos females = 6.215 ± 0.540; Syros males = 11.815 ± 0.994, Syros females = 8.466 ± 0.453).

Local versus non-local conspicuousness

We also verified that our local versus non-local model design was accurate in the experiments conducted on Syros, because local (Syros) models were more camouflaged than non-local (Skopelos) models to avian predators, in terms of chromatic contrast (Fig. 5; $F_{1,40} = 30.497$, $P < 0.001$, $h_p^2 = 0.433$; local = 7.857 ± 0.419 JND versus non-local = 13.433 ± 0.954). However, contrary to our planned design, the reverse was found in the experiments on Skopelos, as local (Skopelos) models were significantly more conspicuous in color than non-local (Syros) models to avian predators, (Fig. 5; $F_{1,64} = 23.341$, $P < 0.001$, $h_p^2 = 0.267$; local = 11.006 ± 0.835 vs. non-local = 5.910 ± 0.521).

Model survival

Survival against all predatory attacks (avian and non-avian)

Attack rates were 26.0% on Skopelos and 25.3% on Syros, when all attacks on models (non-avian and avian) were included in the analysis, with both missing and unat-tacked models classified as censored. As predicted, there was no significant effect of model color treatment on survival of models against combined avian and non-avian predatory attacks on both Skopelos ($W_4 = 5.707$, $P = 0.222$) and Syros ($W_4 = 6.453$, $P = 0.168$). There was a highly significant effect of study site (i.e., where the models were located on each island) on model survival, but only on Skopelos ($W_9 = 24.530$, $P = 0.004$) and not on Syros ($W_9 = 10.074$, $P = 0.345$).

Survival against only avian predator attacks

When only avian attacks were included in the analysis, with both missing and unattacked models classified as censored, attack rates were 10.3% on Skopelos and 7.3% on Syros. On Skopelos, bird attack frequency significantly differed among the model treatments, as predicted ($W_4 = 9.854$, $P = 0.043$). However, contrary to our pre-dictions, there was no significant effect of model treat-ment on survival of models on Syros ($W_4 = 6.592$, $P = 0.159$). Study site (transect) had no significant effect on attack rates on either island (Skopelos: $W_9 = 16.391$, $P = 0.059$; Syros: $W_9 = 3.705$, $P = 0.930$).

Planned comparisons showed that attack frequency by birds was significantly different among male, female, and control models on Skopelos ($W_2 = 9.732$, $P = 0.008$) (Fig. 6A). We found that birds attacked male-colored models significantly more frequently than female-colored models ($W_1 = 8.025$, $P = 0.005$; $\exp(B) = 0.269$) (Fig. 6A). However, the island color type of the models
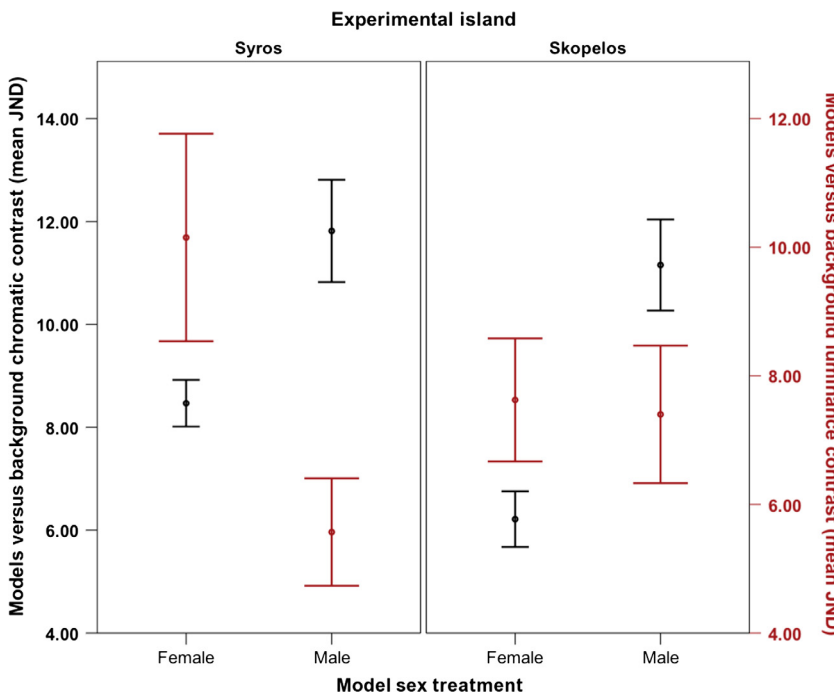

Experimental island

Figure 4. Verification of model design for male and female model treatments. Showing the degree of model versus background contrast of a proportion (18%) of 600 clay models used in the survival experiment. Chromatic (left axis; black data points) and luminance (right axis; red data points) contrast of models against Syros and Skopelos rock backgrounds is shown, as perceived by avian predators (JND). Model treatments were designed to replicate the color and luminance of male and female Aegean wall lizards (*Podarcis erhardii*) from the Syros and Skopelos island populations, calibrated to a typical avian predator (peafowl; *Pavo cristatus*) visual system (*N*: males = 55; females = 53). Generally, values increasing >3.00 JND depict models that are progressively distinguishable against the background. Error bars represent mean JNDs ± 1.0 SE.
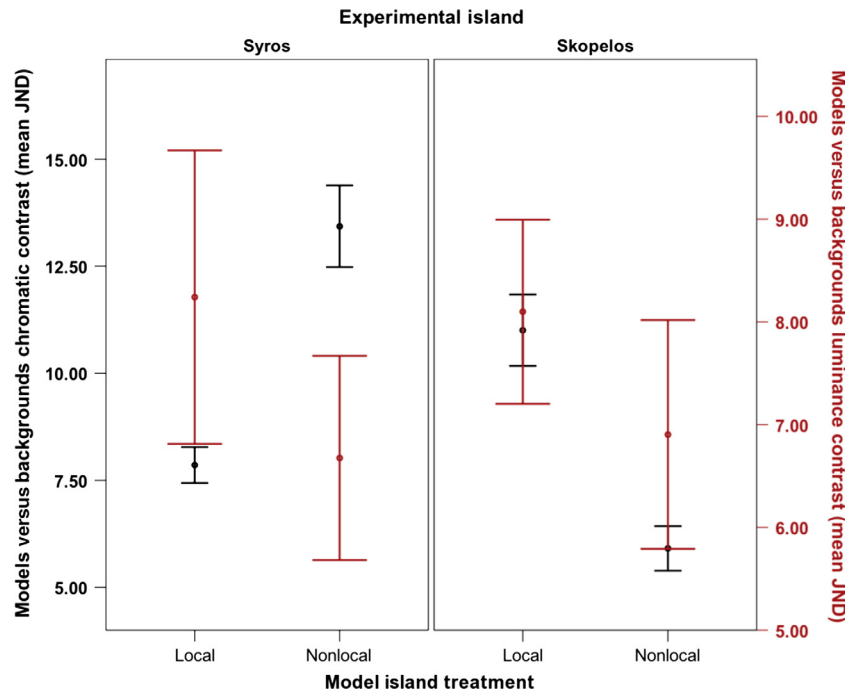
Figure 5. Verification of model design for local versus non-local island model treatments. Showing the degree of model versus background contrast of a proportion (18%) of 600 clay models used in the survival experiment. Chromatic (left axis; black data points) and luminance (right axis; red data points) contrast against Syros and Skopelos rock backgrounds is shown, as perceived by avian predators (JND). Model treatments were designed to replicate the color and luminance of Syros and Skopelos island populations of Aegean wall lizards (*Podarcis erhardii*), calibrated to a typical avian predator (peafowl; *Pavo cristatus*) visual system (*N*: Skopelos = 53; Syros = 55). Model island treatments were local or non-local depending on which island the experiment was performed. Generally, values increasing >3.00 JND depict models that are progressively distinguishable against the background. Error bars represent mean JNDs $\pm$ 1.0 SE.

(i.e., whether they were local (Skopelos) or non-local (Syros)) did not significantly influence attack frequency by birds ($W_2 = 1.380$, $P = 0.502$; Fig. 7). In all analyses, the significance of the results was unchanged when missing models were included (i.e., treated as attacked).

Discussion

Our results show that, on one of the two study islands, models exhibiting sexually dimorphic coloration of Aegean wall lizards (*Podarcis erhardii*) were attacked at different rates by avian predators. This indicates that sexual dimorphism potentially has consequences on survival of the real lizards and that interactions between natural and sexual selection can underlie color variation within a species. As predicted, this was found only against visually oriented avian predators, as non-avian predators (e.g., rodents, snakes) are likely to use olfactory and thermal cues to find prey, making the use of visual cues potentially less important than for birds (e.g., Buning 1983; Vander Wall et al. 2003; Hughes et al. 2010). In all, 35% of attacks were by avian predators. Why the majority of

attacks on models were non-avian is not clear in our study. Although it could indicate that individual birds learned that the models were inedible, this is not substantiated by the relatively high avian attack rate compared to most similar past experiments (e.g., Stuart-Fox et al. 2003 [57%]; Husak et al. 2006 [20%]; Shepard 2007 [2%]; Valkonen et al. 2011 [10%]). Moreover, the low density of models in different, nonadjacent study sites minimized the chances that the same predator would encounter multiple models, and so birds were unlikely to learn that the models were unprofitable.. Instead, past work has indicated that non-avian predators may be attracted to the odor of clay models (Rangen et al. 2000) and that these ground-dwelling predators (i.e., snakes, rodents) may have relatively higher encounter rates with the models than do aerially hunting birds (Husak et al. 2006). In addition, although we did not consider conspecific attacks, we occasionally observed lizards displaying close to the models (personal observations) and noticed possible conspecific attack marks, as in similar past studies (e.g., Husak et al. 2006; McMillan and Irschick 2010). Thus, the role of *P. erhardii* col-
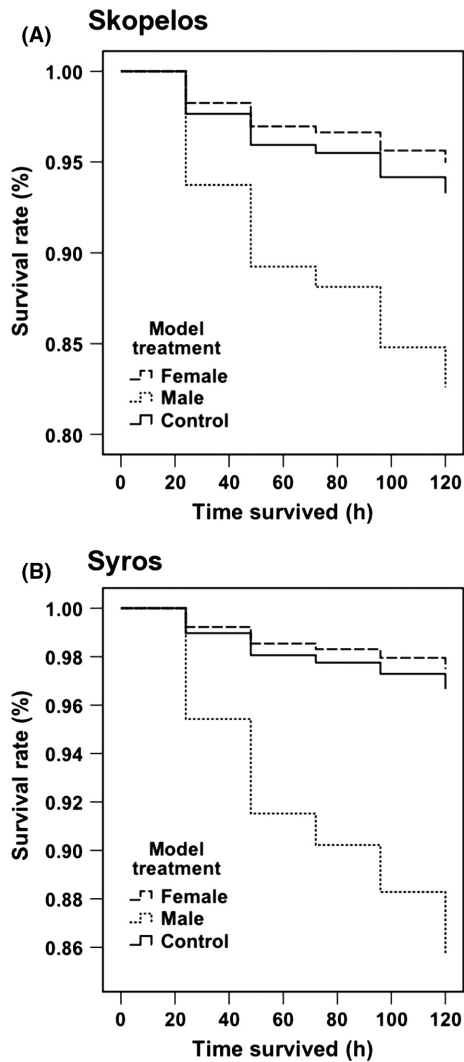
Figure 6. Survival of male versus female models. Showing cumulative survival rate of clay models of Aegean wall lizards (*Podarcis erhardii*) against avian predator attacks on Skopelos (A) and on Syros (B) over five consecutive days. The model treatments were designed to resemble male and female coloration (from both island populations), and a brown control that did not replicate *P. erhardii* coloration (N = 300; males = 120, females = 120, control = 60).

Figure 7. Survival of local versus non-local models. Showing cumulative survival rate of clay models of Aegean wall lizards (*Podarcis erhardii*) against avian predator attacks on Skopelos over five consecutive days. The model treatments were designed to resemble Syros (non-local) and Skopelos (local) island populations (both males and females), and a brown control that did not replicate *P. erhardii* coloration (N = 300; local = 120, non-local = 120, control = 60).

oration in attracting conspecific attacks would be valuable to explore in future experiments.

We found an overall model treatment effect on avian attack rates on only one of the two focal islands (Skopelos). This effect was due to birds detecting and attacking conspicuous male models more frequently than relatively camouflaged female models (Figs 4 and 6A). These results are in line with previous research testing predator attacks on artificial models as a proxy of survival in relation to degree of prey camouflage and conspicuousness (Stuart-Fox et al. 2003; Husak et al. 2006; Stobbe and Schaefer
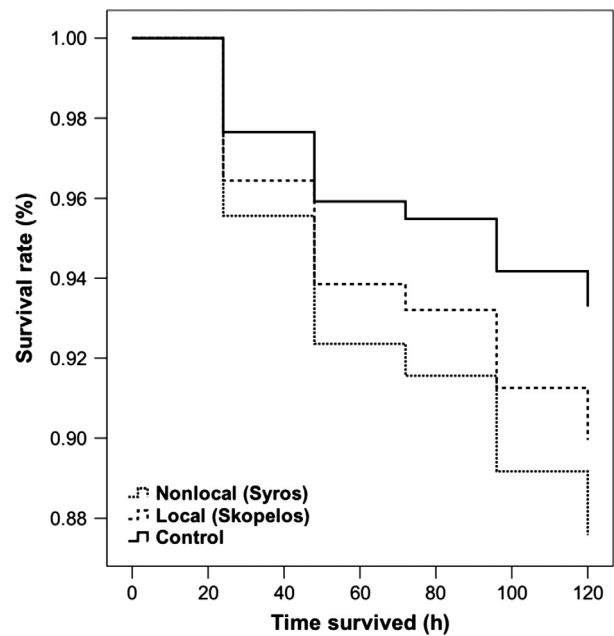
2008; Vignieri et al. 2010; Farallo and Forstner 2012). Why a significant treatment effect was found only on Skopelos was possibly due to the relatively higher frequency of avian attacks on this island (i.e., 10.3% on Skopelos vs. 7.3% on Syros) providing increased statistical power, especially given that the results on Syros showed a similar trend (Figs 4 and 6B).

As shown in previous work (Marshall and Stevens 2014), our findings support the idea that selection has favored more camouflaged coloration in female *P. erhardii*, resulting in their relatively high survival (i.e., low attack rate) against avian predators. In contrast, conspicuousness appears to be more important in males, possibly for intra- and intersexual signaling, particularly as male lizards are known to exhibit conspicuous colors to attract mates and deter rival males, even on more exposed dorsal regions in *P. erhardii* (see Fig. 1; e.g., LeBas and Marshall 2000; Bajer et al. 2010, 2011; Pérez i de Lanuza et al. 2013; Marshall and Stevens 2014). As in previous studies on other lizards (e.g., Stuart-Fox et al. 2003; Husak et al. 2006), we show here that increased conspicuousness in males appears to heighten their risk of detection and subsequent attack by avian predators, although this may be affected by island ecology, such as degree of predation risk (Marshall and Stevens 2014). This may have in turn

favored selection for signal adaptations that offset this risk in local environments, including signal partitioning (Endler, 1992; Stuart-Fox et al. 2004; Garcia et al. 2013; Marshall and Stevens 2014) and local adaptation to enhance camouflage (Stuart-Fox et al. 2004; Rosenblum 2006; Rosenblum et al. 2010; Marshall et al., in press). In *P. erhardii* specifically, previous work has shown that signal partitioning is present in the focal island populations, yet males tend to have relatively conspicuous anterior backs compared to that of females (Marshall and Stevens 2014). The relatively conspicuous backs of *P. erhardii* males may be sufficiently costly to survival to function as "honest" signals of mate quality (Kirkpatrick and Ryan 1991; Schluter and Price 1993; Andersson 1994) particularly in habitats where there is a high risk from avian predators, which would be valuable to explore in future work.

Despite males suffering higher attack rates than females, our results also show that male-colored models maintained a high survival rate against avian predators during the course of the experiment on Skopelos (83% over 5 days). One possible explanation is that avian predators did not recognize the models as prey. However, we suggest that this is unlikely for several reasons. We found a relatively high or at least similar avian attack rate on Skopelos (10.3%) compared to typical avian attack rates in previous predation experiments using artificial prey models (e.g., Stuart-Fox et al. 2003 [8–17%]; Husak et al. 2006 [8%]; Shepard 2007 [1–3%]; Vignieri et al. 2010 [2–5%]; Valkonen et al. 2011 [7–15%]). Although this could potentially be explained by object exploration by birds or an inherent attraction to certain colors, we also found that avian attacks were mostly directed at the head compared to other body regions, as in other similar experiments (e.g., Farallo and Forstner 2012; Table 3), which is consistent with observations of predatory birds tending to attack the head of prey items (Smith 1973, 1976). In addition, we showed that the models occupy a similar area of tetrahedral (avian) color space to that of the real lizards (Fig. 2) and crucially that most model treatments should be hard to distinguish from the average color and luminance of the lizards they were designed to resemble (i.e., ≤3 JND; Siddiqi et al. 2004; Table 1). Taken together, these points suggest that hunting birds did recognize the models as real lizard prey. Instead, the conspicuousness of male dorsal coloration may be sufficiently low to avoid extremely high rates of detection by avian predators, suggesting that male conspicuousness is constrained by the need to be concealed, especially on the more exposed dorsal surface as shown in previous work in lizards, as well as birds, wolf spiders, *Bicyclus* butterflies, and crabs (Stuart-Fox et al. 2004; Stuart-Fox and Ord 2004; Clark et al. 2011; Gluckman and Cardoso 2010; Oliver et al. 2009; Cummings et al. 2008; Garcia

et al. 2013; Marshall and Stevens 2014). Moreover, male coloration is particularly variable in *P. erhardii*, even within island populations (see Fig. 1), which may impair the search efficiency of visually oriented avian predators by preventing them from forming an accurate search image based on color information (Dukas and Kamil 2001; Karpestam et al. 2014).

It is important to note that our measurement of model survival relied on identification of predator attack marks on the models, rather than direct observations of attacks. General avian attacks could be identified in the models and were distinguishable from non-avian attacks (see Fig. 3), as in other survival experiments using clay models (e.g., Castilla and Labra 1997; Husak et al. 2006). However, we cannot rule out that some avian attacks were from bird species with ultraviolet-sensitive (UVS) color vision as well as from birds with violet-sensitive (VS) color vision (i.e., raptors and corvids; Castilla and Labra 1997; Handrinos and Akriotis 1997; Hart et al. 2000; Collar 2005; Cuthill 2006; Sazima and D'Angelo 2011), even though the latter was considered the more important predator type in this study, due to its significance as a major predator of lizards in Europe and in Greece specifically (Handrinos and Akriotis 1997; Castilla et al. 1999). Nonetheless, because our experimental models replicated actual *P. erhardii* coloration as perceived by birds with either a VS or UVS visual system (see Table 1), our findings indicate that sexual dichromatism in *P. erhardii* influences survival against avian predators that possess either class of color vision.

As expected, local models were more camouflaged than non-local models on Syros, which achieved our planned experimental design based on previous work showing that lizards (and mice) are better camouflaged in local than in non-local environments (e.g., Stuart-Fox et al. 2004; Rosenblum 2006; Vignieri et al. 2010; Marshall and Stevens 2014; McLean et al. 2014; Marshall et al., in press). However, this was not the case for models on Skopelos, as local models were unexpectedly more conspicuous than non-local models (Fig. 5). Yet, Skopelos was the only island where we found an effect of model treatment on avian attack rates. Predation rates on Syros alone may not have been high enough and/or model sample sizes may not have been large enough to find a local versus non-local treatment effect. In addition, the models may not have exhibited avian-perceived coloration of the two (local and non-local) populations with sufficient precision. The often extensive dorsal patterning of *P. erhardii* was not replicated, and the models matched only an average of the anterior and posterior dorsal coloration rather than exactly resembling the often variable coloration between the two body regions (see Fig. 1). Although these limitations in our model design may have resulted in biologi-

cally imprecise coloration, it is also possible that birds hunting from a distance may not be able to perceive substantial patterning or variation in color between anterior and posterior dorsal regions, particularly as the lizards are small (i.e., ≈7 cm snout-to-vent length; Arnold and Ovenden 2002). Nonetheless, future work should investigate the role of fine-scale markings and intradorsal color variation on survival.

An alternative explanation is that individual *P. erhardii* may exhibit behavioral preferences for certain backgrounds that improve camouflage (as in ground-nesting Japanese quail, *Coturnix japonica*, Lovell et al. 2013). If this were the case, then the backgrounds we selected for the models might not accurately reflect those local backgrounds favored by the real lizards. Therefore, future work should use lizards' chosen backgrounds as experimental substrates, which could further clarify how local adaptation and behavior underlies color variation. In addition, to fully explore the effects of island ecology on local adaptation of background-matching camouflage in *P. erhardii*, future work needs to investigate a greater range of island populations given that our current study focused on just two populations.

Our key results show that sexual dimorphism may influence risk from avian predators, with males experiencing higher detection and attack rates than females due to increased conspicuousness for costly sexual signaling, as similarly shown in previous work (e.g., Stuart-Fox et al. 2003; Husak et al. 2006). This indicates that coloration and conspicuousness, as well as compromising adaptations such as signal partitioning, can potentially influence survival and be driven by conflicting interactions between natural and sexual selection. However, we found no evidence for the role of local adaptation for camouflage in causing color variation, despite other work suggesting the contrary (e.g., Stuart-Fox et al. 2003, 2004; Rosenblum 2006; Vignieri et al. 2010; Marshall and Stevens 2014; Marshall et al., in press). This was possibly due to limitations in our experimental design. For example, we did not consider that lizards' background choices might affect camouflage and we conducted experiments on only two islands. Thus, further investigation is required. Overall, these results highlight the importance of considering actual predators' perception of coloration and conspicuousness against natural visual backgrounds and how this may influence survival against predators. Further work should examine how the influence of behavioral adaptations, such as escape responses and microhabitat selection, may counteract the increased risk of predator attacks in conspicuous individuals. Furthermore, it would be valuable to explore how different degrees of conspicuousness affect predator attacks, which could help to identify the specific level of conspicuousness that starts to impair survival in different local environments. This research can ultimately reveal how predation risk underlies selection for intraspecific diversification in antipredator defences among distinct local environments.

Acknowledgments

Conflict of Interest

None declared.

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