Journal of Thermal Biology 113 (2023) 103532

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Some like it hotter: Differential thermal preferences among lizard color morphs

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ARTICLE INFO

Keywords:
Aegean wall lizard
Alternative phenotypes
Polymorphism
Podarcis erhardii
Preferred temperature
Thermoregulation

ABSTRACT

Temperature rules the lives of ectotherms. To perform basic biological functions, ectotherms must make behavioral adjustments to keep their body temperatures near a preferred temperature (Tpref). Many color polymorphic lizards are active thermoregulators and exhibit morph differences in traits related to thermoregulation, such as color, body size, and microhabitat use. The Aegean wall lizard, *Podarcis erhardii*, is a heliothermic lizard with orange, white, and yellow color morphs that differ in size, behavior, and microhabitat use. Here, we tested whether *P. erhardii* color morphs from the same population from Naxos island, Greece, differ in Tpref. We hypothesized that orange morphs would prefer lower temperatures than white and yellow morphs because orange morphs are often found on cooler substrates and in microhabitats with more vegetation cover. We obtained Tpref for 95 individuals using laboratory thermal gradient experiments of wild-caught lizards and found that orange morphs do, indeed, prefer cooler temperatures. Average orange morph Tpref was 2.85 °C lower than average white and yellow morph Tpref. Our results add support to the idea that *P. erhardii* color morphs have multivariate alternative phenotypes and present the possibility that thermally heterogeneous environments play a role in the maintenance of color polymorphism in this species.

1. Introduction

More than 98% of all animal species are ectothermic and have strong biological ties to temperature (Angilletta et al., 2002; Angilletta, 2009). To maintain an appropriate body temperature, many ectothermic reptiles thermoregulate by basking in the sun, sheltering in shade, and moving between warmer or colder areas (Cowles and Bogert, 1944; Pough and Gans, 1982). For reptiles, basic biological processes such as growth, digestion, egg production, locomotion, and mating and escape behavior are all affected by body temperature (Huey, 1982; Cooper, 2000). Thus, body temperature is arguably the most important ecophysiological variable for reptiles (Stapley, 2006; Meiri et al., 2013; Garcia-Porta et al., 2019).

Thermal preference represents an important parameter of ectotherms' thermal profiles and has been interpreted as an intrinsic character (Van Damme et al., 1986; Carneiro et al., 2017). Since many of its bodily functions and behaviors are temperature-sensitive, knowing an ectotherm's preferred body temperature is key to understanding many aspects of its life (Taylor et al., 2020). Tpref is also considered a significant ecological index that may be linked to species distributions (Buckley et al., 2010; Crickenberger et al., 2020). In nature, an animal's available range of temperatures is governed by its access to the diversity of microhabitats available to it, including cooler areas near water or in shade or hotter areas in full sun. Many ectotherms, such as insects, snakes, toads, and lizards, exhibit individual variation in their preferred temperatures and microhabitat selection based on their morphologies, coloration, and social behavior (Forsman, 2000; Bittner et al., 2002; Ng et al., 2013; Sanabria et al., 2014).

Intraspecific color morphs with morph-associated morphology, social behaviors, and microhabitat associations have evolved in many

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https://doi.org/10.1016/j.jtherbio.2023.103532
Received 11 November 2022; Received in revised form 23 February 2023; Accepted 23 February 2023

species across the tree of life (Hugall and Stuart-Fox, 2012; Brock et al., 2022c), particularly in lizards (Stuart-Fox et al., 2020). Yet, relatively little is known about intraspecific color morph variation in preferred body temperature (but see Paranjpe et al., 2013; George and Miles, 2022). Indeed, animal color morphs are expected to use different subsets of available resources and occupy different environmental niches due to morph-associated morphological and microhabitat differences (Watt, 1968; Forsman et al., 2008). Color polymorphic lizards provide an opportunity to understand the relationships among color, microhabitat selection, and thermal preference.

Color polymorphism is the evolution of two or more genetically-determined color morphs within a single population (Ford, 1945; Forsman et al., 2008). Lizards from distantly related families have independently evolved similar color morphs that usually have orange, yellow, blue, or white throats (Stuart-Fox et al., 2020; Brock et al., 2022c). Color morphs often differ in more than just color; they may also exhibit differences in other traits, including body size, behavioral and physiological differences, and microhabitat preferences (Gray and McKinnon 2007; Stuart-Fox et al., 2020). When morphs with co-adapted trait complexes, or alternative phenotypes, coexist in a population, they may seek out different microhabitats with different visual properties to maintain crypsis from visual predators or to maximize visual signal efficacy to conspecifics (Leal and Fleishman, 2004; Bond and Kamil, 2006; Maan et al., 2008; Ng et al., 2013). For example, in *Anolis* lizards, signal efficacy for brighter dewlap colors like reds, pinks, and oranges increases in darker, mesic habitats, which are also usually cooler than sunnier, open xeric habitats (Leal and Fleishman, 2004; Ng et al., 2013). If color morphs differ in the brightness of their color patch and occupy distinct microhabitats with different thermal conditions, then morphs may have different temperature preferences and thus exhibit other life history differences.

The Aegean wall lizard, *Podarcis erhardii*, is a color polymorphic lacertid lizard that behaviorally thermoregulates to maintain its body temperature (Belasen et al., 2017; Pafilis et al., 2019; Brock et al., 2020). Like many *Podarcis* lizards, adult *P. erhardii* have three genetically determined throat color morphs that are orange, white, or yellow (Andrade et al., 2019; Brock et al., 2022c, Fig. 1). *Podarcis erhardii* color morphs differ in brightness of their throat color (Brock et al., 2020), body size, behavior (Brock et al., 2022a), and habitat use (BeVier et al., 2022; Brock and Madden, 2022), which are traits that could have implications for morph differences in thermal preferences (Digby, 1955; Forsman, 2000). In general, *P. erhardii* orange morphs and white morphs tend to be most different from each other, and yellow morphs usually exhibit intermediate phenotypes in a suite of physical and behavioral traits (Brock et al., 2020). Orange males are larger than white and yellow males, and female color morphs do not differ significantly in size (Brock et al., 2020), though orange females tend to be on the larger end of the size spectrum. Orange morphs are found more often in microhabitats that have more vegetation and are cooler; in contrast, white and yellow morphs are more often found in areas that are open and hotter (BeVier et al., 2022). In laboratory behavioral experiments conducted on male color morphs, orange morphs were the least bold and aggressive, yellow morphs were intermediate, and white morphs were the most active, aggressive, and adept at winning contests over limited open basking space (Brock et al., 2022a). These differences in *P. erhardii* color morph morphology, microhabitat selection, and social behavior may play a role in their thermoregulatory behavior and thermal preferences. Variation in color morph thermal preferences may have profound implications for color morph life histories and relative color morph fitness in hotter, drier environments.

Fig. 1. A) A white morph *Podarcis erhardii* basking on a dry stone wall, Naxos, Greece. Images of *P. erhardii* orange (B), white (C), and yellow (D) throat color morphs.

Here, we quantified color morph Tpref with thermal gradient experiments to determine whether *P. erhardii* color morphs exhibit different preferred temperatures. We predicted that orange color morphs would prefer cooler temperatures than white and yellow morphs due to their more frequent use of darker, cooler microhabitat. Given their similar choices for microhabitat that is open and hotter (Brock and Madden, 2022; BeVier et al., 2022), we predicted that white and yellow morphs would not exhibit different preferred temperatures from one another.

2. Materials and methods

2.1. Study species

Podarcis erhardii is a small to medium-sized (adult SVL range: 45–75 mm) lacertid lizard (Fig. 1) that is highly variable in color and body size across its discontinuous range comprising hundreds of islands in the Aegean Sea (Marshall et al., 2015; Stadler et al., 2022; Brock et al., 2022b). Adults have one of six genetically-determined throat colors: orange, orange-white, white, white-yellow, yellow, or yellow-orange (Andrade et al., 2019; Brock et al., 2020). We limited our study to the three monochromatic orange, white, and yellow morphs to maximize genetic and phenotypic differences. These color morphs form three identifiable clusters in phenotypic color space according to K-means clustering or linear discriminant function analysis based on spectral reflectance data (Brock et al., 2020). Although there is a small area of potential overlap between the yellow and orange morphs, we only selected lizards for this study that were clearly identifiable as a white, yellow, or orange morph. *Podarcis erhardii* lizard is diurnal and has an activity period from 08:00 to 19:00 in summer, when the days are longest and hottest (Belasen et al., 2017). As its vernacular name suggests, the Aegean wall lizard is commonly found basking on dry stone walls that are common throughout the region.

Podarcis erhardii is endemic to the southern Balkans and is present on many of the Aegean islands, including the Cyclades and Sporades island clusters. This region experiences a classic Mediterranean climate with a long dry period that commences at the end of spring, hot summers, and cool wet winters (Valakos et al., 2008). *Podarcis erhardii* is a generalist that can be found in a variety of habitats, from low-elevation sandy dunes with sparse vegetation, to mid-elevation rocky, dry areas with dense xeric vegetation, all the way up to forested montane habitats reaching 1400 m in elevation (Lymberakis et al., 2018).

2.2. Study area and sampling

In May 2022, we sampled 95 lizards from Naxos island, Greece. Naxos is the largest island in the Cyclades island cluster (land area: 440 km^2) and is the center of *P. erhardii's* distribution in the Aegean Sea. We sampled lizards from the terraced foothills below Profitis Ilias peak (elev. 590 m a.s.l., 37.08043203432896 °N, 25.49171180549804 °E). We chose this site because it features a diverse combination of habitat types that represent the range of thermal microhabitats available throughout the island. The site is located around a remote hiking path bordered by dry stone walls, which also form the terraced agricultural plots at the site. The vegetation at this site consists of a mixed matrix of grasses, phrygana (*Euphorbia acanthothamnos*), olive trees (*Olea europaea*), and sclerophyllous evergreen maquis. This diversity of vegetation, combined with stone walls and hiking paths that wind through hot open areas, provides a range of temperatures for *P. erhardii* to behaviorally thermoregulate.

We sampled only adult lizards (>45 mm SVL) for this study. Lizards were caught with a lasso attached to the end of a telescopic fishing pole. Color morph is discernible by eye in this population (Brock et al., 2020), and one of us (KMB) categorized morphs as orange, white, or yellow in the field upon capture (Corl et al., 2010). Prior to experimentation, we measured lizard snout-vent length (SVL) in mm with a pair of digital calipers (Mitutoyo 500-171-30 Absolute Scale Digital Caliper, Aurora, Illinois, USA) and recorded their mass to the nearest 0.1 g with a digital scale (Pesola PTS3000 Platform Scale, Schindellegi, Switzerland). Female lacertid lizards lack active femoral pores, and so we sexed lizards based on the absence or presence of femoral pores and hemipenes. After preferred temperature experiments, we returned animals to their exact point of capture. The University of California, Berkeley IACUC (protocol AUP-2021-08-14567) and the Greek Ministry of Energy and the Environment (permit ΥΠΕΝ/ΔΔΔ/5619/145) approved animal handling and use protocols used in this study.

2.3. Preferred temperature experiments

We conducted preferred temperature experiments in an air-conditioned room at 19 °C with constant lighting between 8:00 and 20:00. To measure Tpref, we used a specially designed thermal gradient made of cardboard measuring 100 x 44 x 28 cm (Fig. 2). We divided the thermal gradient into four, 11 cm wide lanes, which allowed us to test four lizards simultaneously. Lanes were divided by opaque cardboard so that lizards could not see each other and to reduce the potential effects of visual cues on positioning and thermoregulatory behavior. We positioned heating bulbs in order from left to right of 65 W, 150 W, and 65 W directly over each of the 3 lane dividers at one end of the gradient (Fig. 2). We placed ice packs at the opposite end to create a thermal gradient from 15 °C to 45 °C and confirmed gradient temperatures (measured by thermometer, see Van Damme et al., 1986). While this setup does not discriminate between heat and light source, photothermal gradients are commonly used to measure Tpref (Van Damme et al., 1986, 1989; Qu et al., 2011; Ortega et al., 2016). *Podarcis* lizards are heliothermic and, to the best of our knowledge, do not exhibit photo-tactic response. We covered the floor of the temperature gradient in 1 cm of sand from the island to give lizards traction for free movement and a more natural and familiar substrate. We replaced the sand between every experiment to remove any waste or scents from the previous lizard that might affect thermoregulatory behavior. We did not feed or provide water to lizards prior to experimentation.

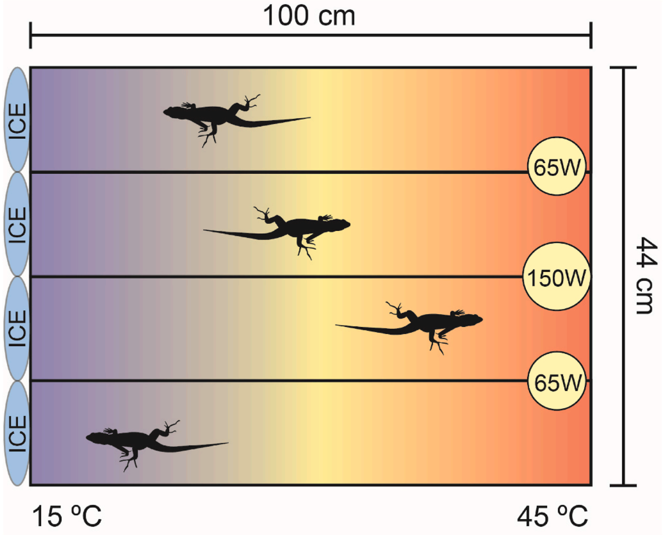

Fig. 2. Diagram of the thermal gradient used to measure Tpref in *P. erhardii*, as viewed from above. The gradient temperature ranged from 15 °C at the cold end to 45 °C at the hot end. The gradient was maintained with ice packs (blue ovals) at the cold end, and heating bulbs of 65 W and 150 W (yellow circles) at the hot end.

To begin a Tpref experiment, we placed a lizard in the middle of a lane and allowed it to habituate to the thermal gradient for 30 min (N = 52) without taking any body temperature measurements (Carretero, 2012; Carneiro et al., 2015; Belasen et al., 2017). For a subset of experiments we extended the acclimation period to 60 min (N = 19) and 120 min (N = 24) to determine if acclimation period significantly affected Tpref. We randomized lane assignments and ran experiments with sets of individuals that varied by morph, sex, and reproductive status. After the habituation period, we took external body temperature measurements with a FLIR TG56 temperature gun (Hare et al., 2007; Trochet et al., 2018; George and Miles, 2022) 5–8 cm away from the lizard every 5 min for 1 h (N = 50), 3 h (N = 24), and 6 h (N = 21). We ran trials of different lengths due to time constraints in the field and accounted for this in our data analysis. To keep body temperature measurements consistent among individuals, we took temperature readings on the dorsal surface between the lizard's shoulders and did not make physical contact. In preliminary experiments (N = 20), a quick-reading thermocouple inserted 5 mm into each lizard's cloaca and taped into place altered their ability to freely move freely through the gradient and their general behavior (e.g., biting the wire, inspecting the wire, and attempting to remove the tape). We verified that measurements taken on the dorsum with the FLIR TG56 temperature gun did not significantly differ from body temperatures taken internally with a quick-reading thermocouple (Supplementary Material). If a lizard moved while we were in the process of taking a surface temperature reading, we marked that measurement N/A. We used each lizard in only one Tpref experiment.

We calculated individual Tpref for each lizard as the 50% interquartile range (IQR) of all body temperature measurements taken while they were in the thermal gradient after the habituation period. When then calculated color morph Tpref as the 50% IQR of all individual Tpref calculations for each color morph.

2.4. Statistical analysis

We used R v4.1.1 for all statistical analyses (R Core Team, 2021). To test for effects of color morph on Tpref while controlling for potential confounding variables, we fit a linear mixed model (LMM) with Tpref as the response variable and a suite of predictor variables: color morph (orange, white, and yellow), sex (female and male), reproductive status (gravid, non-gravid), snout-vent length (SVL), body mass (grams), and habituation period (30, 60, 120 min) as fixed effects, and experiment duration (1 h, 3 h, and 6 h) and lane position in the experimental gradient (1, 2, 3, and 4) as random effects. To identify differences in morph Tpref, we used the Anova(.) function from the 'car' package in R to extract an analysis of deviance table from Type II Wald chi-square tests, followed by a *post hoc* Tukey Honest Significant Difference test.

3. Results

We obtained Tpref estimates for 95 lizards (Table 1). Tpref ranged from 26.5 °C to 40.2 °C (mean = 34.8 ± 1.85 °C) across all individuals. Results from our LMM revealed that color morph was a significant predictor of Tpref (Table 2). Tpref was not significantly associated with sex, mass, SVL, reproductive status, experiment length, lane in the experimental chamber, or habituation period (Table 2). Variance and

Table 1
Color morph, sex, sample size (n), mass, SVL, and Tpref for *P. erhardii* used in this study. Numerical values are presented as mean ± SD.

Morph (n)	Mass (g)	SVL (mm)	Tpref (°C)
Orange (32)	7.99 ± 1.49	65.9 ± 3.41	32.7 ± 2.07
Females (10)	6.66 ± 0.64	64.6 ± 2.30	32.7 ± 1.72
Males (22)	8.59 ± 1.37	66.6 ± 3.69	32.7 ± 2.25
White (31)	6.31 ± 1.43	61.8 ± 4.29	35.5 ± 1.72
Females (14)	5.49 ± 1.29	60.8 ± 4.89	35.4 ± 1.83
Males (17)	6.99 ± 1.18	62.6 ± 3.69	35.5 ± 1.69
Yellow (32)	6.48 ± 1.71	62.2 ± 5.04	35.6 ± 1.99
Females (16)	5.12 ± 1.28	59.0 ± 5.39	35.9 ± 1.58
Males (16)	7.84 ± 0.68	65.3 ± 1.29	35.3 ± 2.34

Table 2
Output from a linear mixed model of *P. erhardii* Tpref. Color morph was the only significant predictor of variation in *P. erhardii* Tpref.

Predictor (fixed effects)	Estimate	Standard Error	*t* value	*P* value
Intercept	37.66	3.84	9.81	**< 0.001**
Morph (white)	2.34	0.55	4.25	**< 0.001**
Morph (yellow)	2.51	0.53	4.71	**< 0.001**
Sex	0.52	0.70	0.75	0.45
Mass	−0.10	0.26	−0.38	0.70
SVL	−0.07	0.08	−0.86	0.39
Reproductive Status	0.61	0.64	0.95	0.35
Habituation period	−0.004	0.005	−0.93	0.36

standard deviation estimates for the random effects (experiment duration and lane) were both <0.0001. We found that preferred temperature (Tpref) differed significantly among color morphs ($P < 0.001$). A post-hoc Tukey HSD test revealed that the orange morphs preferred significantly cooler temperatures than white (orange-white difference = −2.8 °C, $P < 0.001$) and yellow (orange-yellow difference = −2.9 °C, $P < 0.001$) morphs (Fig. 3). White and yellow morph Tpref did not differ significantly (white-yellow difference = −0.14 °C, $P = 0.95$).

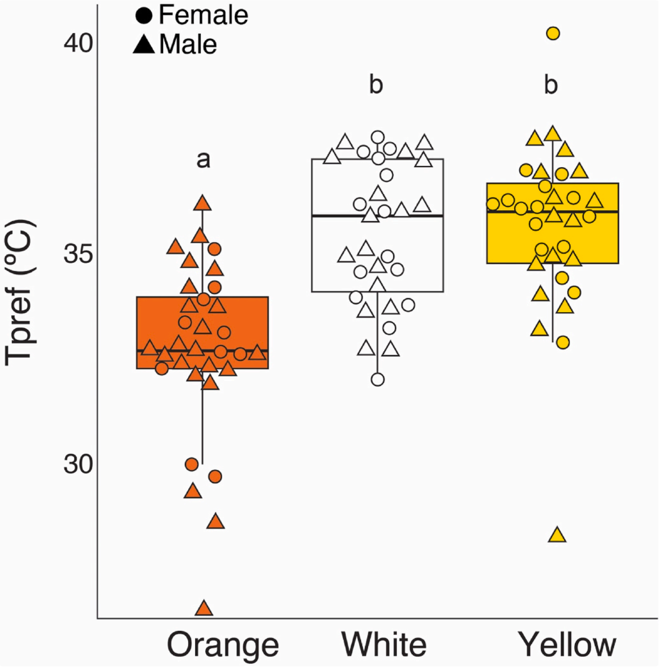

Fig. 3. Thermal preference (Tpref, °C) for *P. erhardii* according to throat color morph (orange, white, yellow). Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), and outermost values within the range of 1.5 times the respective quartiles (whiskers). Values for individual lizards are shown as circles (females) and triangles (males). Significantly different group means are indicated by different letters. Orange morphs have a significantly cooler Tpref compared to white and yellow morphs.

4. Discussion

We found significant support for our hypothesis that orange morphs in *P. erhardii* would prefer cooler temperatures compared to the white and yellow morphs (Fig. 3), which we had based on their observed preference for microhabitats that offer cooler, shadier conditions (BeVier et al., 2022). A hypothesized consequence of color polymorphism is the evolution of morphs that have non-overlapping environmental resource use and distinct thermal physiologies (West-Eberhard, 1986; Galeotti and Rubolini, 2004; Forsman and Åberg, 2008; Forsman et al., 2008). This can be due to a combination of different morph-specific traits, including differences in morph chroma and brightness that determine relative crypsis and visual conspicuousness in different lighting environments, microhabitat selection based on different heating and cooling rates of color morphs, and body size differences (Forsman et al., 1997; Forsman, 2000; Forsman et al., 2008).

In Aegean wall lizards, morph colors are restricted to the throat, which they display to other lizards during social interactions by lifting their head back (Brock et al., 2022a). It is unclear what information these throat color signals contain and how much, if any, effect color variation in this body region has on heating and cooling rates. Previous work in reptiles has shown that dorsal skin pigmentation has significant effects on heating and cooling (Tanaka, 2007; Smith et al., 2016) and that differences in substrate thermal properties can influence ventral color evolution (Goldenberg et al., 2021). Throat color polymorphism has been associated with numerous trait deviations among the different color morphs in *Podarcis* lizards (Calsbeek et al., 2010; Abalos et al., 2016; Brock et al., 2020; Sreelatha et al., 2021), though its significance for thermoregulation remains understudied. Color morph differences in Tpref may have implications for long-term morph coexistence within and among populations, a phenomenon that has intrigued and puzzled biologists for decades (Ford, 1945; West-Eberhard, 1986; Gray and McKinnon, 2007; Corl et al., 2010).

Beyond thermoregulation, coloration in lizards is often associated with social interactions and can sometimes be the byproduct of unrelated cellular or endocrine processes (Smith et al., 2016; Sinervo and Lively, 1996). For example, in color polymorphic Side-blotched lizards (*Uta stansburiana*), brighter orange morphs have higher levels of circulating testosterone, which is associated with morph differences in aggression, territoriality, and reproductive strategies (Sinervo et al., 2000). Testosterone is associated with brighter coloration in various lizard species, including *Sceloporus* (Cox et al., 2008) and *Podarcis* throat color morphs (Huyghe et al., 2009; Sacchi et al., 2017). Future work in color polymorphic species should address the relationship between morph color, hormones, space use, physiological performance, and temperature preference.

In our sample, body size was not a significant predictor of Tpref. Another study on a closely related polymorphic species, *Podarcis gaigeae*, found a relationship between body size and Tpref: larger lizards preferred higher body temperatures (Runemark et al., 2010; Sagonas et al., 2013). However, it is unknown whether or not *P. gaigeae* color morphs differ in body size or thermal preference. Body size may indeed influence lacertid thermoregulation but not in a clear pattern (Ortega and Martín-Vallejo, 2019). Tpref was not significantly associated with body size in our study (Table 2), even though orange morphs tend to be larger (Table 1) suggesting that some other morph-correlated trait, like microhabitat selection (Brock and Madden, 2022), might drive morph differences in Tpref.

Our Tpref results lie within the same thermal range reported in previous studies on *P. erhardii* (Belasen et al., 2017; Pafilis et al., 2019), though orange lizards chose lower Tpref than lizards in these previous studies. Nonetheless, other *Podarcis* species have been shown to select equally low Tpref (Adamopoulou and Valakos, 2005; see Table 2 in

Kapsalas et al., 2016). Former investigations on the thermal biology of the Aegean wall lizard treated all individuals indiscriminately in terms of throat color, in contrast to our study here. We identified only one other study that measured lizard throat color morph Tpref (Paranjpe et al., 2013). Paranjpe et al. (2013) found that yellow morph females in the Side-blotched lizard have significantly hotter preferred body temperatures than females from the yellow-orange and orange morphs (Paranjpe et al., 2013). Side-blotched lizards and wall lizards are distantly related, yet color morphs exhibit a similar pattern of temperature preference. Our findings and those of Paranjpe et al. (2013) demonstrate that color morphs do differ in thermal traits and pave the way for further investigation of the thermoregulation of the species. If color morph is considered, future research may reveal distinct thermoregulatory effectiveness depending on the morph.

In other color polymorphic species, including fish, birds, and lizards, intraspecific color morphs occupy distinct light environments to maintain crypsis, avoid predation, and maximize color signaling efficacy (Galeotti et al., 2003; Gray and McKinnon, 2007). For example, in the Indonesian fish *Telmatherina sarasinorum*, male color morphs experience visual environment-contingent sexual selection (Gray et al., 2008). Certain color morphs of *T. sarasinorum* are more conspicuous at different water depths, and thus their space use and frequencies vary across their visually heterogeneous environment (Gray et al., 2008). A comparative analysis of owls, nightjars, and raptors found that color polymorphic species in these groups tend to live in more diverse habitats with open and closed microhabitats compared to monomorphic species (Galeotti and Rubolini, 2004). Environmental resource partitioning, such as occupying different thermal conditions or light environments, should reduce intraspecific competition and allow for the maintenance of multiple alternative phenotypes within a single population (Forsman and Åberg, 2008). This is common at the interspecific level and evident in other lacertid species that partition their thermal habitat to reduce interspecific competition (Scheers and Van Damme, 2002; Pafilis et al., 2017; Sagonas et al., 2017), but it might also be the case for conspecifics belonging to different color morphs. While morph differences in microhabitat related to light environment are well-described, less is known about morph differences in microhabitat use based on thermal conditions. In *P. erhardii*, orange morphs tend to stay close to shady vegetation and use vegetation as refuge more often than white and yellow morphs (Brock and Madden, 2022). Indeed, over several years of fieldwork in the Cyclades islands, we have found brighter orange morphs in more closed, highly vegetated microhabitats (BeVier et al., 2022; Brock et al., 2022b).

If there are constraints on microhabitat availability, variation in color morph preferred body temperature may have consequences on relative color morph fitness, especially for an ectotherm like *P. erhardii*, due to many temperature-dependent biological functions, like metabolic rate, digestion, growth, and reproduction (Bennett and Dawson, 1976; Pafilis et al., 2007). Thermal preferences may also affect the geographical distribution of the color morphs. We tend to find few or no orange morphs on the hottest, driest islands with little environmental heterogeneity in the Cyclades (Brock et al., 2022b). If environmental conditions consistently favor a certain morph over others, non-favored morphs may go extinct, and favored morphs become fixed in the population (West-Eberhard, 1986; Forsman et al., 2008; Corl et al., 2010; Massot et al., 2010). However, the mechanisms by which morph fixation occurs are not well understood. Across 44 different locations in the Cyclades, *P. erhardii* orange morphs seem to be lost first from 10 islands where only yellow and white morphs remain, one island is fixed for the yellow morph, and 19 islands have white morph fixation (Brock et al., 2022b). Morph loss appears to happen in an ordered fashion - first orange, then yellow, with only one exception. Parallel ordered morph loss across many *P. erhardii* populations from hot, dry islands could be the result of directional selection that favors morphs who do well under those conditions. Future research in this system should investigate morph thermal physiology and the thermal properties of morph microhabitats to determine the relative availability of those microhabitats across different islands. If orange morphs are tied to cooler, wetter environments, they may not be able to persist where those conditions are unavailable.

Overall, our results provide more evidence that *P. erhardii* color morphs exhibit differential thermal preferences and have may utilize different environmental resources (BeVier et al., 2022; Brock and Madden, 2022; Brock et al., 2022a), potentially on the basis of morph-specific trait variation. The results of our study suggest that morph thermal preference may be driven, at least in part, by differences in microhabitat use or preference. For ectotherms, in particular, distinct intraspecific morph temperature preferences have myriad implications for how morphs behave and interact (Brock et al., 2022a) as well as their growth rates, physiological performance, reproductive output, and relative morph fitness in different environments (Angilletta et al., 2002; Sinervo and Adolph, 1994; Autumn and De Nardo, 1995; Gray et al., 2008). The extent to which different temperature-dependent physiological processes differ between color morphs with different preferred temperatures could have a major influence on how color polymorphism evolves, persists, or erodes. Morph differences in social, sexual, and antipredator behavior may be related to their preferred body temperatures, and future research should investigate these relationships using a combination of observations from natural populations and laboratory studies. The role of thermally heterogeneous environments in the evolution of color morph thermal physiology and the maintenance of color polymorphism should also be explored further.

CRediT authorship statement

Asher Thompson – Methodology, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Visualization, Funding Acquisition. Vassiliki Kapsanaki – Investigation, Writing – Review & Editing. Heather E.M. Liwanag – Methodology, Writing – Review & Editing. Panayiotis Pafilis – Resources, Writing – Review & Editing. Ian J. Wang – Writing – Review & Editing. Kinsey M. Brock – Methodology, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Visualization, Supervision, Funding Acquisition.

Funding sources

A.T. was supported by a travel grant, a summer internship grant, and faculty-initiated research project funds from the Rausser College of Natural Resources SPUR program at the University of California, Berkeley. This work was funded by the National Science Foundation PRFB (Award Number 2109710) awarded to K.M.B.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

Data will be found on Dryad under the title of our paper and the author name Kinsey Brock once we are assigned a manuscript number from J Therm Bio

Acknowledgements

We thank Dhruthi Mandavilli, Serey Leakna Nouth, Tanmayi Patharkar, and Jerry Sun for their assistance with catching lizards. We thank the Wang Lab (Anusha Bishop, E. Anne Chambers, Jess McLaughlin, Dan Oliviera, and Erin Westeen) for their helpful feedback on drafts of this manuscript. We thank Dr. Donald Miles for his insights and fun conversations about lizard color morphs. Thanks to John Adams, whose "*The Dharma at Big Sur*" propelled our writing. A.T. was supported by a travel grant, a summer internship grant, and faculty-initiated research project funds from the Rausser College of Natural Resources SPUR program at the University of California, Berkeley. This work was funded by the National Science Foundation PRFB (Award Number 2109710) awarded to K.M.B.

Appendix ASupplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2023.103532.

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