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Colour morph predicts social behaviour and contest outcomes in a polymorphic lizard (*Podarcis erhardii*)

Kinsey M. Brock [a, b, *], Marie-Claire Chelini [c], Cole Ayton [a], Indiana E. Madden [a, d], Cynthia Ramos [a], Jessica L. Blois [a], Panayiotis Pafilis [e, f], Danielle L. Edwards [a]

[a] *Life & Environmental Sciences, School of Natural Sciences, University of California, Merced, CA, U.S.A.*
[b] *Quantitative & Systems Biology Graduate Program, School of Natural Sciences University of California, Merced, CA, U.S.A.*
[c] *Departments of Biology and Evolutionary Anthropology, School of Arts and Sciences, Duke University, Durham, NC, U.S.A.*
[d] *School of Veterinary Medicine, University of California, Davis, CA, U.S.A.*
[e] *Department of Zoology, National and Kapodistrian University of Athens, Athens, Greece*
[f] *Zoological Museum, National and Kapodistrian University of Athens, Athens, Greece*

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Space is a limited resource in which many animals need to perform basic functions such as feeding and reproducing. Competition over access to space can induce a variety of behaviours that may result in differential access to crucial resources related to survival and fitness. The Aegean wall lizard, *Podarcis erhardii*, is a colour-polymorphic lizard that inhabits dry stone walls where they access food, safely thermoregulate, shelter from predators and interact with other lizards. Many colour-polymorphic species have morphs with distinct behavioural strategies, which may play a role in morph evolution and maintenance. Here, we conducted the first behavioural experiments on *P. erhardii* colour morphs. Our goal was to compare morph competitive ability and characterize morph differences in social behaviours using laboratory contest experiments over limited heated space on a stone wall in a neutral arena. Contest experiments revealed that colour morph, not size, predicted intermorph contest outcomes. White and yellow morphs were associated with winning and the orange morph was associated with losing contests. Male colour morphs exhibited different levels of aggressive, boldness, chemical signalling and visual signalling behaviours depending on which morph they were in contest with. White morphs always performed aggressive and scent-marking behaviours more frequently during contests with other morphs. Yellow morphs performed aggressive, bold, chemical signalling and visual signalling behaviours at intermediate frequencies relative to other morphs. Orange morphs performed aggressive behaviours equally often when in contest with yellow morphs but performed all other behaviours less frequently against yellow and white morphs. Considering these results, behavioural variation among *P. erhardii* colour morphs may promote morph maintenance.

Colour-polymorphic species are ideal systems for understanding how phenotypic variation evolves and is maintained within populations (Ford, 1945; Gray & McKinnon, 2007). Colour polymorphism is the presence of two or more genetically determined colour phenotypes within a single interbreeding population (Huxley, 1955) and has been identified in a wide range of taxa, from invertebrates to birds (Jamie & Meier, 2020). Intraspecific colour morphs often, if not always, exhibit additional differences in traits besides colour (McKinnon & Pierotti, 2010; Stuart-Fox et al., 2020), such as morphology (Brock et al., 2020), physiology (Huyghe et al., 2009) and behaviour (Sinervo & Lively, 1996). These multitrait differences between colour morphs can evolve via correlational selection, whereby genetic correlations of certain combinations of heritable traits are favoured (Roulin, 2004). A mystery surrounding alternative morph phenotypes in natural populations is their long-term maintenance: how does colour polymorphism persist in the face of natural selection and other evolutionary forces such as genetic drift, which tend to reduce genetic variation in populations (Roulin, 2004; Runemark et al., 2010)? Although polymorphic species may differ in the number of colour morphs and the kinds of morph-correlated traits, a prevailing similarity across these systems is that morph diversity is maintained by some type of

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[*] Corresponding author.
E-mail address: kbrock@berkeley.edu (K. M. Brock).

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balancing selection for alternative multivariate morph phenotypes (reviewed in: Gray & McKinnon, 2007; Stuart-Fox et al., 2020). Thus, identifying morph-correlated traits and the contexts in which they function is essential for understanding how colour polymorphism and phenotypic diversity, in general, is maintained within populations.

In many colour-polymorphic species, colour morphs exhibit morph-specific behavioural strategies (Barcelo-Serra et al., 2020; Brodie, 1992; Dijkstra et al., 2008; Kupper et al., 2016; Sinervo et al., 2000; Sinervo & Lively, 1996). Often, these morph-specific behavioural strategies are under correlational selection and involved in predator avoidance or reproduction, and thus, have fitness consequences (Brodie, 1992; Kupper et al., 2016). The relative frequency of morphs within a population can remain at a stabilized equilibrium, but in many colour-polymorphic systems, morph frequencies oscillate through time (Gross, 1991; Olendorf et al., 2006; Sinervo & Lively, 1996). Interactions between morphs can generate balancing or frequency-dependent selection that maintain the polymorphism within the population (Dijkstra et al., 2008; Iversen et al., 2019; Sinervo & Lively, 1996), although the nature of these interactions varies widely among populations and from species to species (Bastiaans et al., 2013; Lattanzio & Miles, 2014). Understanding how colour morphs interact is an important step towards identifying alternative morph strategies and mechanisms that influence morph fitness, frequencies and maintenance.

Access to resources such as suitable space, food and mating opportunities is crucial for animal survival and reproduction (Andersson, 1994). If morphs have different abilities to access resources that enhance fitness, those behaviours may influence the frequency of morph alleles in colour-polymorphic populations (Sinervo & Lively, 1996). High levels of aggression and exploratory behaviour (e.g. boldness) are often associated with dominance and greater reproductive success (Ficken et al., 1990; Kingston et al., 2003). Colour morphs in birds (Gouldian finch, *Chloebia gouldiae*: Pryke, 2006; white-throated sparrow, *Zonotrichia albicollis*: Horton et al., 2012), lizards (common wall lizard, *Podarcis muralis*: Abalos et al., 2016) and fish (Midas cichlid, *Cichlasoma citrinellum*: McKaye & Barlow, 1976) distinctly vary in levels of aggression. Moreover, morph colour can signal information about competitive ability to the receiver (Bruinjé et al., 2019). These visual signals could also be used differently depending on whether the receiver belongs to the same or a different colour morph. In some species, morphs use different levels of aggression and aggressive behaviours in competitive situations based on morph colour (Scali et al., 2021; Tinghitella et al., 2018; Yewers et al., 2016). In many instances, male morphs exhibit aggression bias and are more likely to attack individuals of the same colour morph (Dijkstra et al., 2008; Horton et al., 2012; Scali et al., 2021; Yewers et al., 2016). Same-morph aggression bias could generate a frequency-dependent advantage for the morph at the lowest frequency in the population, since it would experience overall lower levels of aggression (Seehausen & Schluter, 2004). Nevertheless, negative interactions such as competition and territoriality are not the only interactions that may shape coexistence and evolution (Kamath & Wesner, 2020). Colour morphs may use visual signals in combination with other traits, such as chemical signals (López et al., 2009), to discern morph types and identify situations in which it is advantageous to yield, cooperate or share (Sinervo & Lively, 1996; Smith & Price, 1973). Studies that simultaneously evaluate different kinds of colour morph behaviours and morph interactions can help us understand how colour morph diversity is maintained in nature.

The Aegean wall lizard, *Podarcis erhardii* (Bedriaga, 1882), is a colour-polymorphic lacertid lizard with multiple discrete colour morphs in both sexes. Females and males have throat badges that are orange, yellow or white (Brock et al., 2020). Female colour morphs within a population do not differ in body size or head dimensions, but orange males have significantly larger body and head sizes than yellow and white male morphs (Brock et al., 2020). Body size and mass have strong relationships with resource-holding potential and the ability to persist in contests (Arnott & Elwood, 2009; Huyghe et al., 2009; Parker, 1974). Due to differences in head size dimensions, male *P. erhardii* colour morphs also have different bite force capacities (Brock et al., 2020), which is a known predictor of contest and reproductive success in lizards (Husak & Fox, 2008; Huyghe et al., 2009; McLean & Stuart-Fox, 2015). The larger orange morph tends to bite harder than the yellow and white morphs, which do not differ in their maximum bite force capacities (Brock et al., 2020). Furthermore, orange and white male morphs in this species have significantly different proportions of chemical compounds in exudate secreted from their femoral pores (Brock et al., 2020). These secretions can be used for myriad signalling functions in lacertids (reviewed in Martín & López, 2014), including territory demarcation (Aragón et al., 2001), male rival assessment (López & Martín, 2002) and female choice (Gabirot et al., 2013). Most *Podarcis* wall lizard species are colour polymorphic (Brock, McTavish, & Edwards, 2022), and male morphs in *Podarcis* species can have different levels of aggression, hormones and chemical signal profiles (Abalos et al., 2016; Brock et al., 2020; Huyghe et al., 2009; Mangiacotti et al., 2019). However, few studies have examined potential morph differences in their ability to access limited resources like thermally suitable habitat, and experiments quantifying multiple types of behaviours outside of pure aggression, such as visual and chemical signalling, are limited (but see Bruinjé et al., 2019; McLean & Stuart-Fox, 2015).

Here, we conducted the first study on colour morph behaviour in *P. erhardii*. Our aim was to identify morph-specific behavioural strategies that may play a role in the maintenance of diverse phenotypes within a population. To do this, we staged one-on-one contests between adult males in an arena with a small stone wall heated to the preferred temperature of *P. erhardii* surrounded by suboptimal colder open ground to determine each morph's ability to maintain access to the limited stone wall resource and to observe the social behaviours of each colour morph during intra- and intermorph contests. We quantified aggressive, bold, chemical signalling and visual signalling behaviours and the duration of stone wall access in experimental contests to answer three main questions. (1) Does colour morph predict an individual's ability to win one-on-one contests over a limited resource? (2) Do adult male *P. erhardii* colour morphs perform aggressive, bold, chemosensory and visual signalling social behaviours at different frequencies during contests? (3) Do morphs exhibit significantly higher levels of aggression towards morphs of the same colour?

We hypothesized that morph colour would predict contest outcomes over a limited thermally optimal space resource. Specifically, we predicted that the orange morph would tend to win more contests against white morphs and yellow morphs, due to their larger size in nature (Brock et al., 2020). Larger body size is often associated with higher levels of testosterone and aggressive behaviour in male lizards (Arnott & Elwood, 2009; Donihue et al., 2016; Huyghe et al., 2009). We hypothesized that colour morphs would exhibit social behaviours at different frequencies during staged contests since colour morph phenotypes often differ in morphology and behaviour (Abalos et al., 2016; G. C. Carpenter, 1995; Huyghe et al., 2009; Sinervo & Lively, 1996). Specifically, we predicted that white morphs would perform chemosensory behaviours more frequently than other morphs and would perform fewer aggressive behaviours because the unique chemical profile in their femoral pore exudate and their smaller body size in nature (Brock et al., 2020) may result in a strategy where they access space by avoiding conflict and denoting their occupancy with scent marks. We predicted that yellow morphs would perform visual signalling behaviours more frequently than other morphs to convey their morph colour and status since their throat colour is intermediate and their body size and chemical signal profile somewhat overlap with both white and orange morphs (Brock et al., 2020). We also predicted that yellow morphs would exhibit an overall intermediate strategy compared to white and orange morphs. We predicted that the orange morph would perform more aggressive and bold behaviours more frequently than other morphs since male orange morphs in *P. erhardii* can bite harder than other morphs (Brock et al., 2020) and, in other colour-polymorphic lizard species such as *Podarcis melisellensis* (Huyghe et al., 2009), *Ctenophorus decresii* (Yewers et al., 2016) and *Uta stansburiana* (Sinervo et al., 2000), orange morphs have higher levels of testosterone and aggression. Finally, we hypothesized that colour morphs would exhibit higher levels of aggression with morphs of the same colour compared to morphs of different colours (Dijkstra et al., 2008; Horton et al., 2012; Scali et al., 2021), which could potentially play a role in balancing colour morph frequencies in colour-polymorphic populations (Scali et al., 2021; Seehausen & Schluter, 2004).

METHODS

Study Species

Podarcis erhardii is a small lacertid species with an adult snout–vent length (SVL) of 45–80 mm and a tail twice as long as the body (Valakos et al., 2008). *Podarcis erhardii* is endemic to the southern Balkans and has a distribution that stretches across southern Bulgaria, north Macedonia, southern Serbia, Albania and Greece, including hundreds of Aegean islands (Valakos et al., 2008). This species occurs in a variety of habitats ranging from low-lying rocky desert islets at sea level, sandy arid shores, mixed low spiny vegetation and grasses and montane forest regions up to 2000 m in elevation. As their vernacular name suggests, these lizards are typically found on dry stone walls where they can access food items, prominently display to conspecifics and thermoregulate close to refuge. *Podarcis erhardii* is diurnal and most active during 0800–1200 hours and 1600–1900 hours in spring and summer. The *P. erhardii* breeding season typically lasts from April to June.

As an ectotherm, *P. erhardii* behaviourally thermoregulates and requires access to basking spaces at their preferred temperature to maintain homeostasis and perform basic physiological functions (Belasen et al., 2017; Pafilis et al., 2019). *Podarcis erhardii* has also been observed on dry stone walls performing other behaviours such as hunting (Donihue, 2016), laying down chemical signals (Brock et al., 2020), escaping and avoiding predation (Brock et al., 2015; Li et al., 2014), mating (K. M. Brock, personal observation) and fighting (Madden & Brock, 2018) across many island environments. Throughout its range, *P. erhardii* is known to engage in intense intraspecific aggressive physical behaviour such as biting that leaves scars (Brock et al., 2015; Donihue et al., 2016), finger and tail consumption, and even cannibalism (Donihue et al., 2016; Madden & Brock, 2018). The extent to which individuals within populations of *P. erhardii* differ in behaviours such as aggression, boldness and signalling behaviours has yet to be explored.

Sampling

We conducted our study on Naxos, the largest Cycladic island located in the central Aegean Sea. Adult male lizards were captured from a single population near the agricultural village of Moni on Naxos island (37°04′54.1″N, 25°29′35.0″E) in May 2018. We chose this population for its abundance of lizards, presence of all three colour morphs and diverse habitat with mixed vegetation that also contained a plethora of dry stone walls. The encounter rates of colour morphs in this population at the time of sampling were 10% orange, 32.6% yellow and 57.4% white (218 total lizards, including males and females). Lizards were captured with a thread lasso attached to the end of an extendable fishing pole. We sexed lizards immediately upon capture by visually assessing the presence of enlarged femoral pores, a swollen tail base and a larger block-shaped head (indicative of males). We determined lizards as mature adult males if they had an SVL (length spanning the tip of the nose to the vent) larger than 45 mm (SVL range 55.41–71.12 cm, $N = 60$). We captured 60 lizards, 20 of each colour morph (orange, yellow, white). Lizards were placed in individual cloth bags and transported to the laboratory on Naxos for further measurement, temporary housing and experimentation.

Animal Housing and Husbandry

Lizards were housed individually in plastic terraria (20 × 40 cm and 20 cm high) with sand substrate gathered from their home site in Moni. Each terrarium contained a water dish and two large stones used in classic dry stone wall construction for thermoregulation and refuge. Each terrarium was situated under a 40 W incandescent lamp and received 12 h of light per day. Light and temperature cycles were set to mimic field conditions (12 h of light from 0700 to 1900 hours, 15 °C average at night, 26 °C average during the day). Lizards were provided full-spectrum light (Zoo Med ReptiSun 10.0 UVB Compact Fluorescent Mini Reptile Lamp, 13 W, Zoo Med, San Luis Obispo, CA, U.S.A.) thrice per week for 2 h to prevent metabolic bone disease (Adkins et al., 2003). We covered all walls adjacent to other terraria with opaque paper to shield lizards from viewing their neighbours and minimize stress. Lizards were fed a diet of mealworms (*Tenebrio molitor*) dusted with Zoo Med Repti Calcium once per day and given water ad libitum. Lizards were given 1 week to acclimate to laboratory conditions before experiments commenced, and they stayed in the laboratory for a total of 1 month before being released back to their exact capture location in Moni.

Ethogram

Prior to experimentation, we generated an ethogram to catalogue social behaviours exhibited by adult male lizards from our study population in their natural habitat (Table 1). Over 4 days, we conducted direct observations in the field during peak hours of activity (0800–1700 hours) from a distance with binoculars to limit effects of our presence on the subjects' natural behaviour. We narrowed the list of potential behaviours in our ethogram to discrete, countable actions that were repeatedly observed in nature and could be readily identifiable during experimental contests (Table 1).

We assigned behaviours to four categories: aggression, boldness, chemosensory and visual signalling (Table 1), although we acknowledge some signalling behaviours may serve multiple functions or overlap slightly between categories. We measured how frequently lizards used these different categories of behaviours in experimental contests with specific colour morphs to better understand morph-specific interactions and competitive ability.

Experimental Contest Design, Arena Set-up and Quantification of Behaviour

We staged 90 30-minute contests between two lizards in a neutral arena where neither morph had a potential residency advantage (Abalos et al., 2016). Each contestant competed against

Table 1
Ethogram of contest behaviours exhibited by adult male *P. erhardii*

Behaviour	Description	Context	Category
Bite	Bites opponent	Biting, chasing, gaping and lunging are regularly described asaggressive behaviours in lizards (Abalos et al., 2016; Stamps, 1977; Yewers et al., 2016). Biting and lunging involve physical contact that can intimidate and injure another lizard and are usually assigned higher point values when scoring aggressive behaviour (Stamps, 1977; Yewers et al., 2016). Chasing in lizards is often used to physically remove another individual from the area (C. C. Carpenter, 1961). Lizards often gape at each other to convey the power of their bite and/or intention to attack (Abalos et al., 2016; Lappin et al., 2006)	Aggression
Chase	Quickly follows opponent		
Gape	Opens mouth wide towards opponent		
Lunge	Hits opponent using its head, with a fast, forward motion		
Approach	Walks towards opponent	To initiate an interaction with another lizard (approach) and walk the perimeter of the stone wall (patrol), lizards expose themselves to conspecifics and/or potential predators. Exploratory behaviours such as these are facets of boldness in lizards (Carter et al., 2012)	Boldness
Patrol	Walks the perimeter of the top of the stone wall		
Mouth wipe	Rubs the length of the side of the mouth on substrate	Lizards wipe their mouths and flick their tongues to sense chemical signals (Jenssen et al., 1995) and wipe their femoral pores on substrates to mark their scent (Carazo et al., 2007). These behaviours are facets of chemosensory communication in lizards	Chemosensory
Pore wipe	Rubs femoral pores on substrate		
Tongue flick	Flicks tongue out of mouth		
Hand wave	Lifts hand in a circular, waving motion	We categorized hand waving, lateral displays, tail displays and throat displays as visual signals because these behaviours can be used to visually communicate multiple kinds of messages to conspecifics (Marshall & Stevens, 2014). Hand waving is used as a pursuit-deterrent signal and as a signal of speed (Baird et al., 2004; Font et al., 2012). Lateral displays can be used to communicate size and are correlated with fighting ability (C. C. Carpenter & Grubitz, 1961; Marshall & Stevens, 2014) and may also signal vitality. Tail displays can serve multiple functions such as distracting the receiver, deflecting attack and pursuit deterrence (Cooper, 2002). Throat displays in *Podarcis* differ distinctly from head bobbing and push-up displays that are common in other lizard families (Yewers et al., 2016), as it is not a repetitive motion, nor do lizards elevate themselves on all four legs. hroat displays could be used to convey morph colour and head size (K. M. Brock, personal observation)	Visual signalling
Lateral display	Orients body perpendicular to opponent and dorsolaterally flattens to display colourful blue side patches to opponent		
Tail display	Wriggles tail at opponent		
Throat display	Tilts head back and exposes throat to opponent		

the two other colour morphs and its own colour morph for a total of three contests per individual. We designed contests to minimize potential effects of body size and contest order on contest outcome (Baird, 2013; Huyghe et al., 2005; Sacchi et al., 2009). First, we size-matched contestants by measuring their SVL and allowed up to 10% difference in body size between contestants (Baird, 2013). Once contestants were size-matched for their three contests, we randomized the order of contests so that the order of morph encounters was uncoupled from contest order.

The arena consisted of a 60 × 60 cm open top square with a floor and 20 cm high walls constructed with laminate-coated particle board (Appendix, Fig. A1). The arena contained a pile of stones in the middle that functioned as a dry stone wall. The stone wall was approximately 20 × 20 cm and 10 cm high. Two heat lamps were fixed to opposite sides of the arena and pointed at a 45° angle directly at the stone pile resource, simulating a sunny basking spot on a dry stone wall. This species has a preferred temperature of 34 ± 1 °C (Belasen et al., 2017). Thus, temperature on the illuminated stone wall was kept at 34 °C, while the surrounding corners of the arena were a consistent 17 °C to motivate lizards to access the warm rock pile. Contestants were placed in opposite corners of the arena behind an opaque wall of laminated particle board for 5 min so that their starting body temperatures were within 1.5 °C of each other and cooler than the heated stone wall. We used a FLIR TG56 spot infrared thermometer gun to noninvasively measure lizard body temperature during the acclimation period. The removable wall was a 15 × 15 cm cube with an open top and bottom. The wall provided a 15 × 15 cm floor space for contestants to acclimate in private. Both contestants were placed in the arena at the same and given the same amount of time to acclimate behind the wall. At the end of the 5 min acclimation period, we removed the walls from the arena simultaneously and started the 30 min timer. At the end of 30 min, lizards were removed from the arena and placed back in their individual terraria. The entire arena, including the stone wall, was sanitized with 80% ethanol between contests to remove scent marks.

We recorded each contest using a digital video camera (JVC full HD Everio, 120 frames/s recording speed) for postexperimental analysis. All contests occurred between 0800 and 1700 hours in the laboratory under standardized lighting conditions. We used our ethogram to score the number of behaviours performed during each contest. The amount of time an individual spent on the heated rock wall during the 30 min contest was calculated postexperiment from the video data. To minimize reviewer bias, all video data were scored by the same observer (C. Ayton). We defined the ‘winner’ of a contest as the individual who spent the most time (absolute time in seconds) on the heated rock wall.

Ethical Note

All research was conducted in accordance with the University of California, Merced Institutional Animal Care and Use Committee (IACUC protocol AUP17-0002) and permits provided by the Greek Ministry for Environment and Energy (Ω8Δ84653Π8-ΒΞΧ assigned to K.M. Brock). We took several measures to minimize stress and prevent injury before, during and after behavioural experimentation.

Pre-experimentation measures

We kept lizards in separate terraria with their own water dish, food and hide shelter. Terraria were filled with sand from the site where lizards were captured. Per our IACUC protocol, we checked on the wellbeing of lizards three times per day, ensuring that they ate their food, drank water and slept. No lizards were exhausted or lethargic during the light period when in captivity.

During experiments

Given the nature of the behavioural repertoire of the lizards, aggression was an element that was observed during the staged contests as well as some behaviours that may have created injury (such as biting). Observations of such were integral to the study. However, we minimized escalation of stress by (1) keeping the duration of the staged encounters short and (2) before contests began, we had a protocol in place to stop the trials if lizards bit another lizard for longer than 5 s in order to prevent injury. No animals bit for longer than 5 s, bled or died during the experiments or appeared overly stressed (e.g. all lizards continued eating, drinking and sleeping during their time in the laboratory and passed all of their thrice-daily wellbeing checks).

Postexperimentation

At the end of the contest, lizards were immediately removed from the experiment and put back in their individual terraria. Lizards were fed and checked on three times per day to make sure they were eating and acting normally. No animals were permanently or mortally wounded while in our care. All animals were returned to their exact point of capture.

Statistical Analyses

To test whether colour morph predicts intermorph contest outcome, we used a binomial generalized linear mixed model (GLMM) with a logit link function. We modelled contest outcome as a binary ‘win’ or ‘lose’ response variable with morph and percentage difference in contestant SVLs as fixed effects and individual identity (ID) as a random effect, since every individual was involved in two intermorph contests. Residuals were normally distributed (Kolmogorov–Smirnov test: $D = 0.06$, $P = 0.75$) and had equal variance (Levene's test: $F_{2,117} = 1.45$, $P = 0.24$), and thus met the assumptions of binomial GLMM (Schielzeth et al., 2020).

To test for colour morph differences in the ability to retain a limited resource during intermorph contests, we used *t* tests comparing the amount of time morphs spent on the heated rock wall during each contest. Time data for each morph were assessed for normality using Shapiro–Wilk and *F* tests. Time data for all intermorph contests were normally distributed (Shapiro–Wilk tests: yellow versus orange: yellow: $W = 0.885$, $P = 0.214$; orange: $W = 0.925$, $P = 0.123$; orange versus white: orange: $W = 0.926$, $P = 0.135$; white: $W = 0.957$, $P = 0.487$; white versus yellow: white: $W = 0.925$, $P = 0.125$; yellow: $W = 0.951$, $P = 0.381$). Time data for yellow versus orange and white versus yellow contests had equal variances (*F* test: yellow versus orange: $F_{19,19} = 0.563$, $P = 0.219$; white versus yellow: $F_{19,19} = 1.583$, $P = 0.326$), so we proceeded with two-way *t* tests. Orange and white lizard time data had unequal variances (*F* test: orange versus white: $F_{19,19} = 0.219$, $=P = 0.01$), so we used a Welch's *t* test for orange versus white intermorph contests.

To test for morph differences in the frequencies of aggressive, bold, chemical signalling and visual signalling behaviours by contest type, we used chi-square goodness-of-fit tests. We counted the number of aggressive, bold, chemosensory and visual signalling behaviours each morph performed by contest type and used chi-square tests to determine whether morphs performed behaviours at equal frequencies. The chi-square statistic is distribution free and does not require equal variances among groups or homoscedasticity.

To determine whether morphs exhibit higher levels of aggression towards like morphs, we quantified an aggression score for both males in each inter- and intramorph contest. Following other studies in lizards (Abalos et al., 2016; McLean & Stuart-Fox, 2015), we used a 4-point system for different aggressive behaviours. The most aggressive behaviour, biting, was given the highest point value, 4, followed by lunging, chasing and gaping, which were given point values of 3, 2 and 1, respectively. Aggression scores were calculated by summing the total number of points per individual per contest. Colour morph aggression scores had equal variances (Levene's test: orange: $F_{2,57} = 1.66$, $P = 0.19$; white: $F_{2,57} = 0.11$, $P = 0.90$; yellow: $F_{2,57} = 0.36$, $P = 0.69$) but were not normally distributed (Shapiro–Wilk test: orange: $W = 0.83$, $P < 0.001$; white: $W = 0.82$, $P < 0.001$; yellow: $W = 0.89$, $P < 0.001$). Thus, we compared aggression scores by contest type with Kruskal–Wallis tests followed by Dunn post hoc tests.

We used R (v.1.1.456) to conduct all statistical analyses. We used the ‘glmer’ function in the ‘lme4’ package to construct GLMMs (Bates et al., 2015). We used the ‘testResiduals’ function in the ‘DHARMa’ package to verify model assumptions for binomial GLMMs were met (Hartig, 2021). We used the ‘leveneTest’ function in the ‘car’ package to test for equal variances among groups (Fox & Weisberg, 2019). We used the ‘stats’ package for all other analyses (R Core Team, 2013). We set a significance level $\alpha = 0.05$ a priori and used this cutoff for all analyses.

RESULTS

Colour Morph and Contest Outcomes

We could identify a winner in all 90 contests, 60 of which were intermorph contests (orange versus white, white versus yellow, yellow versus orange) and 30 of which were intramorph contests (orange versus orange, white versus white, yellow versus yellow). Out of 60 lizards, nine lost all three contests. Of the nine lizards that lost all three contests, seven were orange, one was white and one was yellow. Seven lizards won all three contests: two orange, three white and two yellow. Only 10 lizards won their two intermorph contests: six white morphs and four yellow morphs. Only eight lizards won the intramorph contest: four orange morphs, one white morph and three yellow morphs. Overall, the white morph won the most intermorph contests (white morph win count = 16/20 versus orange, 11/20 versus yellow), followed by the yellow morph (yellow morph win count = 9/20 versus white, 13/20 versus orange). Counter to our predictions, the larger orange morph won the fewest intermorph contests (orange morph win count = 4/20 versus white, 7/20 versus yellow).

Colour morph predicted intermorph contest outcomes over a limited space resource in a neutral arena (Table 2). White and yellow morphs were associated with winning (Pearson correlation:

Table 2

Relationships between contest outcome, morph and the percentage difference in snout–vent length (SVL) in intermorph contests ($N = 60$ contests)

Contest outcome binomial GLMM	Fixed effect				Variance (±SD) random effect = ID
	Estimate	SE	*Z*	*P*	
Intercept	−0.91	0.44	−2.05	**0.04**	0.08 (±0.26)
White	1.74	0.54	3.23	**0.001**	
Yellow	1.19	0.51	2.37	**0.018**	
% Difference SVL	−1.26	4.11	−0.31	0.76	

The model included individual lizard identification (ID) as a random effect. Significant results are shown in bold.

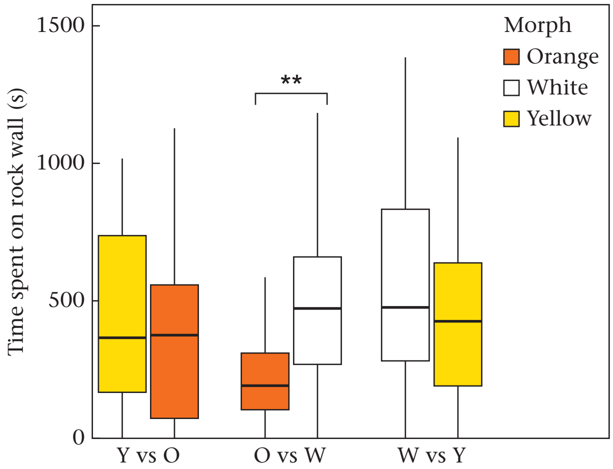

Figure 1. Amount of time morphs spent on the heated stone wall during intermorph contests by contest type. Y = yellow morph; O, orange morph; W, white morph. $^{**}P < 0.01$ (Welch's *t* test).

white: $r_{115} = 1.74$, $P < 0.01$; yellow: $r_{115} = 1.19$, $P < 0.05$), and the percentage difference in SVL between contestants was not significantly associated with contest outcome (Table 2).

Colour morphs varied in the amount of time they spent accessing the heated stone wall in intermorph contests (Fig. 1). In orange versus white contests, we found that white morphs occupied the heated stone wall space significantly longer than orange morphs (Welch's *t* test: orange versus white: $t_{29.224} = -3.363$, $P = 0.002$). In white versus yellow and yellow versus orange intermorph contests, morphs did not significantly differ in the cumulative amount of time spent on the heated stone wall (*t* test: white versus yellow: $t_{38} = 1.285$, $P = 0.207$; yellow versus orange: $t_{38} = -0.853$, $P = 0.399$). On average, white morphs spent 280 s longer occupying the resource than orange morphs in white versus orange contests, yellow morphs spent 102 s longer on the resource than orange morphs in yellow versus orange contests and white morphs spent 146 s longer on the resource than yellow morphs in white versus yellow contests.

Morph Differences in Behaviour Frequencies

Aggression

Colour morphs performed aggressive behaviours at different frequencies in intermorph contests (Fig. 2, Table 3). In yellow versus orange contests, yellow morphs bit, chased and lunged more times than orange morphs, and orange morphs gaped more times than yellow morphs. However, we did not detect significant differences between yellow and orange morphs in the overall frequencies of aggressive behaviours in yellow versus orange contests (Table 3). In orange versus white contests, orange morphs performed all aggressive behaviours fewer times than white morphs. Overall, orange morphs performed aggressive behaviours significantly less frequently than white morphs in orange versus white contests (Table 3). In white versus yellow contests, white morphs bit, chased and lunged more times than yellow morphs, and yellow morphs gaped more times than white morphs. Overall, white morphs performed aggressive behaviours significantly more frequently than yellow morphs in white versus yellow contests (Table 3).

Colour morphs performed aggressive behaviours at different frequencies in intramorph contests. White morphs performed aggressive behaviours significantly more frequently in white versus white contests than orange and yellow morphs did in their intramorph contests (Table 3).

Boldness

Colour morphs performed bold behaviours at different frequencies in intermorph contests (Fig. 2, Table 4). In yellow versus orange contests, yellow morphs approached and patrolled more times than orange morphs. Overall, yellow morphs performed bold behaviours significantly more frequently than orange morphs in yellow versus orange contests (Table 4). In orange versus white contests, orange morphs performed all bold behaviours fewer times than white morphs. Overall, orange morphs performed bold

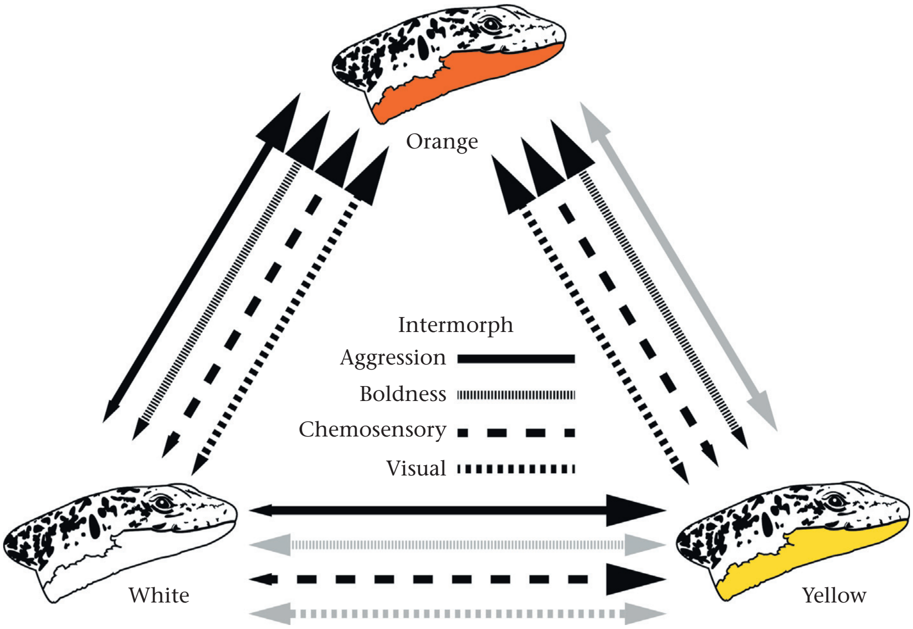

Figure 2. Summary of behaviours colour morphs performed by contest type. Arrows indicate directionality of behaviours. Morphs with small arrowheads pointing at them and big arrowheads pointing away from them indicate that they performed that category of behaviour more frequently than the other morph. Grey arrowheads of equal size indicate no statistical difference between morphs in the frequency of that behaviour category.

Table 3

Chi-square goodness-of-fit tests on frequency of morph aggressive behaviours in inter- and intramorph contests

Contest type	Bite	Chase	Gape	Lunge	Aggressive behaviours		Difference (Obs − Exp)	Chi-square goodness of fit
					Observed	Expected		
Y vs O	Y=7	Y=13	Y=12	Y=31	Y=63	60	Y=3	$\chi^2_1=0.3$, $P=0.584$
	O=3	O=2	O=26	O=26	O=57		O=−3	
O vs W	O=17	O=18	O=39	O=47	O=121	158	O=−37	$\chi^2_1=17.3$, **$P<0.001$**
	W=52	W=26	W=49	W=68	W=195		W=37	
W vs Y	W=33	W=8	W=34	W=58	W=133	116.5	W=16.5	$\chi^2_1=4.67$, **$P=0.03$**
	Y=10	Y=6	Y=39	Y=45	Y=100		Y=−16.5	
O vs O	9	6	20	20	55	106.66	−51.66	$\chi^2_2=101.71$, **$P<0.001$**
Y vs Y	17	9	11	37	74		−32.66	
W vs W	33	14	89	55	191		84.34	

Y, yellow; O, orange; W, white. Significant deviations from equal frequencies are shown in bold.

Table 4

Chi-square goodness-of-fit tests on frequency of morph boldness behaviours in inter- and intramorph contests

Contest type	Approach	Patrol	Bold behaviours		Difference (Obs − Exp)	Chi-square goodness of fit
			Observed	Expected		
Y vs O	Y=126	Y=153	Y=279	247	Y=32	$\chi^2_1=8.29$, **$P=0.004$**
	O=90	O=125	O=215		O=−32	
O vs W	O=169	O=150	O=319	375.5	O=−56.5	$\chi^2_1=17$, **$P<0.001$**
	W=220	W=212	W=432		W=56.5	
W vs Y	W=191	W=233	W=424	366	W=58	$\chi^2_1=18.38$, **$P<0.001$**
	Y=132	Y=176	Y=308		Y=−58	
O vs O	139	45	184	312.66	−128.66	$\chi^2_2=84.06$, **$P<0.001$**
Y vs Y	153	197	350		37.34	
W vs W	234	170	404		91.34	

Y, yellow; O, orange; W, white. Significant deviations from equal frequencies among morphs are shown in bold.

behaviours significantly less frequently than white morphs in orange versus white contests (Table 4). In white versus yellow contests, white morphs performed all bold behaviours more times than yellow morphs. Overall, white morphs performed bold behaviours significantly more frequently than yellow morphs in white versus yellow contests (Table 4).

Colour morphs performed bold behaviours at different frequencies in intramorph contests. White morphs approached each other more times than other morphs, and yellow morphs patrolled the stone wall more times than other morphs in intramorph contests. White morphs performed bold behaviours significantly more frequently in white versus white contests than orange and yellow morphs did in their intramorph contests (Table 4).

Chemical Signalling and Sensing

Colour morphs performed chemosensory behaviours at different frequencies in intermorph contests (Fig. 2, Table 5). In yellow versus orange contests, yellow morphs wiped their mouths and femoral pores on the stone wall and flicked their tongues more times than orange morphs. Overall, yellow morphs performed bold behaviours significantly more often than orange morphs in yellow versus orange contests (Table 5). In orange versus white contests, orange morphs performed all chemosensory behaviours fewer times than white morphs. Overall, orange morphs performed chemosensory behaviours significantly less frequently than white morphs in orange versus white contests (Table 5). In white versus yellow contests, white morphs wiped their mouths on the stone wall and flicked their tongues more times than yellow morphs, and yellow morphs wiped their femoral pores on the stone wall more times than white morphs. Overall, white morphs performed chemosensory behaviours significantly more frequently than yellow morphs in white versus yellow contests (Table 5).

Colour morphs performed chemosensory behaviours at different frequencies in intramorph contests. White morphs wiped their mouths and femoral pores on the stone wall more times in intramorph contests than orange and yellow did in their intramorph contests. Yellow morphs performed tongue flicks more times in yellow versus yellow contests than orange and white morphs did in their intramorph contests. Overall, the white morphs

Table 5

Chi-square goodness-of-fit and Fisher exact tests of frequencies of chemosensory behaviours performed by colour morphs in inter- and intramorph contests

Contest type	Mouth wipe	Pore wipe	Tongue flick	Chemosensory behaviours		Difference (Obs − Exp)	Chi-square goodness of fit
				Observed	Expected		
Y vs O	Y=38	Y=59	Y=1	Y=98	75.5	Y=22.5	$\chi^2_1=13.41$, **$P<0.001$**
	O=24	O=29	O=0	O=53		O=−22.5	
O vs W	O=33	O=41	O=2	O=76	144.5	O=−68.5	$\chi^2_1=64.95$, **$P<0.001$**
	W=93	W=110	W=10	W=213		W=68.5	
W vs Y	W=112	W=30	W=8	W=150	121.5	W=28.5	$\chi^2_1=13.37$, **$P<0.001$**
	Y=59	Y=31	Y=3	Y=93		Y=−28.5	
O vs O	27	36	2	65	112.66	−47.66	$\chi^2_2=118.48$, **$P<0.001$**
Y vs Y	45	9	12	66		−46.66	
W vs W	90	116	1	207		94.34	

Y, yellow; O, orange; W, white. Significant deviations from equal frequencies among morphs are shown in bold.

performed chemosensory behaviours significantly more frequently in white versus white contests than orange and yellow morphs did in their intramorph contests (Table 5).

Visual Signalling

Colour morphs performed visual signalling behaviours at different frequencies in intermorph contests (Fig. 2, Table 6). In yellow versus orange contests, yellow morphs performed hand waves, lateral displays and throat displays more times than orange morphs, and orange morphs performed more tail displays more times than yellow morphs. Overall, yellow morphs performed visual signalling behaviours significantly more frequently than orange morphs in yellow versus orange contests (Table 6). In orange versus white contests, orange morphs performed all visual signalling behaviours fewer times than white morphs. Overall, orange morphs performed visual signalling behaviours significantly less frequently than white morphs in orange versus white contests (Table 6). In white versus yellow contests, white morphs performed lateral displays and tail displays more times than yellow morphs, and yellow morphs performed hand waves and throat displays more times than white morphs. Overall, we did not detect significant differences between white and yellow morphs in the overall frequencies of visual signalling behaviours in white versus yellow contests (Table 6).

Colour morphs performed visual signalling behaviours at different frequencies in intramorph contests. White morphs performed visual signalling behaviours significantly more frequently in white versus white contests than orange and yellow morphs did in their intramorph contests (Table 6).

Inter- versus Intramorph Aggression Scores

On average, none of the colour morphs exhibited significantly higher levels of aggression towards like morphs (Fig. 3). The only significant differences in aggression levels by contest type that we detected were in orange morphs, which exhibited significantly higher aggression scores in contests with white morphs compared to orange or yellow morphs (Kruskal–Wallis chi-square test: $\chi^2_2 = 9.25$, $P_{adj} < 0.001$; post hoc Dunn test: orange versus white – orange versus orange: $Z = -2.52$, $P = 0.02$; orange versus orange – yellow versus orange: $Z = 0.21$, $P_{adj} = 0.84$; yellow versus orange – orange versus white: $Z = 2.73$, $P_{adj} = 0.019$). White morphs had higher aggression scores in all contest types, on average (Fig. 3), but their aggression scores did not significantly differ among contest types (Kruskal–Wallis chi-square test: $\chi^2_2 = 1.82$, $P = 0.40$). Yellow morphs did not differ in aggression scores by contest type (Kruskal–Wallis chi-square test: $\chi^2_2 = 1.35$, $P = 0.51$).

DISCUSSION

Results from our behavioural experiments on *P. erhardii* colour morphs show that male morphs differ in their ability to win staged contests and in the frequency with which they display different social behaviours. We found that colour morph predicted contest outcome over a limited heated space on a stone wall; the winners and losers, however, were not who we expected based on findings from other colour-polymorphic lizards and previous work on *P. erhardii* (Brock et al., 2020). White and yellow morphs were associated with winning intermorph contests, and the orange

Table 6
Chi-square goodness-of-fit tests of frequencies of visual signalling behaviours performed by colour morphs in inter- and intramorph contests

Contest type	Hand wave	Lateral display	Tail display	Throat display	Visual signal behaviours		Difference (Obs − Exp)	Chi-square goodness of fit
					Observed	Expected		
Y vs O	Y=76	Y=7	Y=2	Y=212	Y=297	251	Y=46	χ^2_1=16.86, **P <0.001**
	O=39	O=1	O=20	O=145	O=205		O=−46	
O vs W	O=69	O=6	O=19	O=151	O=245	363.5	O=−118.5	χ^2_1=77.26, **P <0.001**
	W=165	W=24	W=47	W=246	W=482		W=118.5	
W vs Y	W=86	W=16	W=36	W=103	W=241	240.5	W=0.5	χ^2_1=0.002, P=0.96
	Y=99	Y=4	Y=18	Y=119	Y=240		Y=−0.5	
O vs O	40	0	9	118	167	339	−172	χ^2_2=274.48, **P <0.001**
Y vs Y	210	2	25	32	269		−70	
W vs W	125	45	32	379	581		242	

Y, yellow; O, orange; W, white. Significant deviations from equal frequencies among morphs are shown in bold.

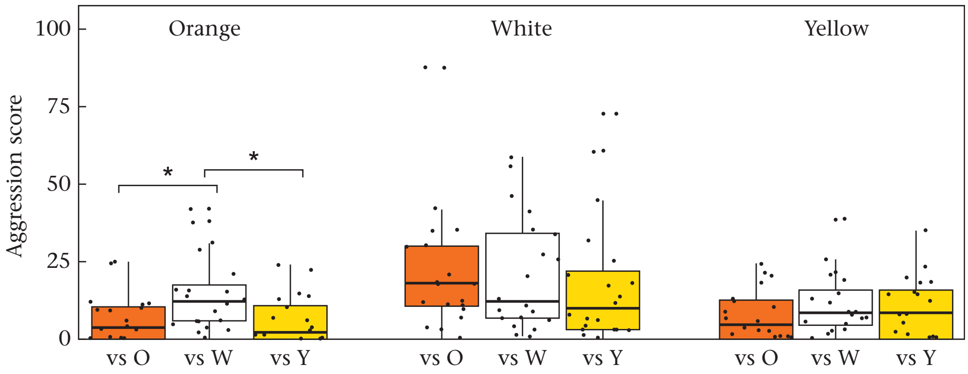

Figure 3. Colour morph aggression scores by contest type. O, orange morph; W, white morph; Y, yellow morph. Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles). $^*P < 0.05$.

morph, which tends to be bigger and bite harder (Brock et al., 2020), was associated with losing intermorph contests. We found that colour morphs indeed performed aggressive, boldness, chemical signalling and visual signalling behaviours at different frequencies, and the frequencies of these behaviours varied by contest type. Finally, we did not find support for our hypothesis that colour morphs are more aggressive towards morphs of the same colour. Overall, our results demonstrate morph-specific divergence in social behaviours and the potential for alternative morph behavioural strategies in this species.

Morph Colour as a Predictor of Contest Outcome

Winning contests over space are pivotal for male reproductive success, as females are often attracted to high-quality habitat (Olsson et al., 2013) and often remain within these certain spaces regardless of individual male presence (Edsman, 2001). Counter to our expectations based on the morphology of this species and contest outcomes related to body size and bite strength in other lizards (Brock et al., 2020; Huyghe et al., 2009; Lappin et al., 2006), the larger orange morph lost more contests for thermally suitable space against white morphs and yellow morphs. We constrained lizard body differences to an upper end of 10% in our contest experiments and found that morph colour was a better predictor of contest outcome than contestant differences in body size. Many examples from contest experiments in squamates suggest that larger body size and stronger bite force is associated with winning contests (Andersson, 1994; Huyghe et al., 2009; West-Eberhard, 1983) as well as elevated levels of testosterone and aggression (Huyghe et al., 2009). In nature, lizards are not size-matched, and similar observations should be collected from colour morph interactions in wild populations to fully understand morph fitness consequences of contest outcomes over mates and quality habitat. It is possible that orange morphs may benefit from their size advantage in a natural setting where smaller white morphs and yellow morphs might not challenge larger orange morphs. Nevertheless, our results do match a recent set of morph behavioural experiments conducted in *P. erhardii*'s close relative, *P. muralis*, where orange morphs also tend to lose intermorph contests to white morphs and yellow morphs (Abalos et al., 2016). A similar pattern exists in a more distantly related colour-polymorphic lizard: in *Urosaurus ornatus*, larger orange-throated male colour morphs also tend to be less aggressive and lose contests to smaller green morphs and blue-green morphs (G. C. Carpenter, 1995; Hover, 1985). This pattern diverges from male colour morphs in *C. decresii*, *Ctenophorus pictus* (Healey et al., 2007) and *U. stansburiana* (Sinervo & Lively, 1996), where orange-throated males exhibit higher levels of aggression and win more contests than other morphs. Studying convergence and divergence in lizard polymorphisms and colour morph traits holds promise for gaining novel insights into the evolution and maintenance of phenotypic variation (Stuart-Fox et al., 2020).

Associations between Morph Colours and Behaviour during Staged Contests

Behavioural differences among colour morphs

Alternative multivariate phenotypes are common among colour-polymorphic species, particularly in lizards (Stuart-Fox et al., 2020). Male *P. erhardii* colour morphs are associated with morphological, performance and chemical signalling traits (Brock et al., 2020), which could arise from multivariate correlational selection for nonrandom trait combinations and generate multiple stable phenotypic optima (Calsbeek et al., 2010; McKinnon & Pierotti, 2010; Sinervo et al., 2001). In contrast, we found that morphs also differ in several categories of social behaviour and that morph matters not only for winning contests over space, but also for the types of interactions that morphs engage in with each other. We found that the orange morph was associated with lower levels of aggression and boldness in an experimental setting. The white morph was associated with boldness and aggression. White morphs approached contestants much more frequently to initiate interactions, patrolled the stone wall more often and displayed elevated levels of scent-marking behaviours. The yellow morph, which has an intermediate throat colour and chemical signal profile (Brock et al., 2020), seemed to also be somewhat of an intermediate between orange and white in aggressive, boldness, chemosensory and visual signalling behaviours. These alternative behavioural phenotypes matched morph contest outcomes, where shy orange morphs, which performed fewer aggressive, visual signalling and scent-marking behaviours, lost more contests over the basking resource against more active white morphs and yellow morphs, which performed significantly more aggressive, bold and scent-marking behaviours. Correlational selection may produce morph-phenotypic variation in morphology and behaviour, and the correlated traits we have identified in *P. erhardii* colour morphs here and in previous work (Brock et al., 2020) are likely involved with additional factors like female choice and morph–environment interactions. For example, in males from this study population, white colour morphs tend to have the smallest SVLs and head sizes (Brock et al., 2020) compared to orange males and yellow males, which females may not prefer. Therefore, white morphs may use a bolder and more aggressive behavioural strategy where they patrol spaces that they mark frequently with their scent, which has lower levels of octadecanoic acid (an indicator of good health; Martín et al., 2007; Martín et al., 2008) than orange morphs (Brock et al., 2020). Orange morphs could gain some fitness advantage for engaging in fewer aggressive interactions and avoiding contests over basking space by expending less energy on male–male interactions and more energy in attracting mates with its size, colour and chemical signal that contains higher proportions of compounds that are associated with attractiveness in other lacertids (Kopena et al., 2011, 2014). Yellow male morphs, which have intermediate body size, head size and chemical signal from their pore exudate (Brock et al., 2020), may adjust their behaviour depending on the colour of neighbouring male morphs (Horton et al., 2012; Yewers et al., 2016) or the relative frequency of other morphs (Sinervo & Lively, 1996). Further behavioural research that incorporates interactions between sexes will help determine how orange morphs, which are associated with losing contests and seem to be the rarest morph in many populations (K. M. Brock, personal observations), persist.

Behavioural differences between intramorph and intermorph contests

One hypothesis regarding rare morph persistence in polymorphic species is like-morph aggression bias, where morphs of the same colour are more aggressive towards each other than other morphs, thereby releasing the rarest morph from high levels of harassment, which may confer a fitness advantage (Scali et al., 2021). We did not find that morphs were more aggressive towards morphs of the same colour. Like-morph aggression is a pattern that has been observed in other colour-polymorphic species and evoked as a mechanism that maintains colour morph diversity (Dijkstra et al., 2008; Horton et al., 2012; Scali et al., 2021; Yewers et al., 2016). We performed our behavioural experiments at the height of the breeding season when hormones associated with aggression like testosterone are usually circulating at peak seasonal levels in males (Belliure et al., 2004). However, it is possible that levels of testosterone and aggression vary differently throughout the seasons in male colour morphs (Sacchi et al., 2017). The relative levels of testosterone in male *P. erhardii* colour morphs at any point during their active period are currently unknown. Further research into the role of testosterone and how it mediates reproductive behaviour (both sexual and aggressive) in *P. erhardii* colour morphs could shed light on the impacts of inter- and intrasexual communication and competition on relative colour morph frequencies and persistence in populations.

Other Factors to Consider in Future Studies

The source population of lizards from Moni had higher frequencies of white morphs during opportunistic sampling trips in the breeding season during 2017–2019 and 2021 (K. M. Brock, personal observations), followed by yellow morphs, and orange morphs were consistently the least common. In fact, white morphs were the most common in 10 different populations across the island of Naxos, the island where we performed our study. Geographical variation in morph frequencies is common, if not the norm in colour-polymorphic species (reviewed in McLean & Stuart-Fox, 2014). In some populations on Naxos, we failed to find any individual of the orange morph. These orange-less populations tended to occur in hot and dry habitats, with sparse vegetation and far from a water source. Although we designed our experiment to motivate lizards to compete over a limited space kept at this species' preferred temperature (Belasen et al., 2017), it is possible that the conditions we created in the experimental set-up were advantageous to certain morphs over others. In other colour-polymorphic species, it is not uncommon for environment-associated morphs to evolve (spiny orb weaver spiders, *Gasteracantha fornicata*: Kemp et al., 2013; cichlids (*Gasterosteus aculeatus*): Tinghitella et al., 2018). In *P. muralis*, a close relative in the same genus as *P. erhardii*, there seems to be a partial divergence in colour morph microhabitat use, where orange morphs tend to prefer humid environments that are close to water (Pérez i de Lanuza & Carretero, 2018). Furthermore, a distribution-wide study of the side-blotched lizard, *U. stansburiana*, found that the yellow morph, which is the least aggressive, is the first morph in that species to be lost from populations (Corl et al., 2010). A range-wide geographical survey of more than 40 isolated island populations of *P. erhardii* found that the least aggressive orange morph was always the least common morph encountered in the population (Brock, Madden et al., 2022). More in situ behavioural observations and research into morph microhabitat use and morph diversity across many populations will provide further insights into morph-correlated traits and morph maintenance within and between populations.

Colour morphs must maintain a minimum viable number of alleles in a population, or else those morphs will die out. So, what maintains the orange morph in natural populations? Negative frequency-dependent selection from processes such as intraspecific competition (Scali et al., 2021; Seehausen & Schluter, 2004) and sexual selection (Sinervo & Lively, 1996), which confer an advantage to rare morphs, could balance colour morph frequencies through time and maintain colour morph diversity (Gray & McKinnon, 2007; Svensson, 2017). Negative frequency-dependent sexual selection, where rare morphs obtain more matings and eventually increase in frequency (Sinervo & Lively, 1996), may be involved in long-term maintenance of colour morph diversity in *P. erhardii*. No long-term studies have yet been conducted in this species to assess morph frequencies in populations from year to year. Long-term field studies that document colour morph frequencies through time and mate choice experiments will be necessary to explore the possibility that negative frequency-dependent selection plays a role in colour morph maintenance.

One advantage the orange morph may hold is an honest signal of health quality, which is used in mate choice by females (Brock et al., 2020). Pigment-based animal coloration, like that in colour-polymorphic *Podarcis* lizards (Andrade et al., 2019), which ranges from red to yellow, has been demonstrated to be an honest signal of individual quality and a predictor of fitness in birds (Ng et al., 2013; Pryke et al., 2010), fish (Grether, 2000) and lizards (Fitze et al., 2009). Additionally, chemical signals play an important role in lizard communication and can be used by females and males to judge competitive ability and dominance status (López & Martín, 2002). Orange and white *P. erhardii* males have significantly different throat colours and chemical signals in the waxy cuticle excreted from their femoral pores (Brock et al., 2020). Orange males have higher proportions of alpha-tocopherol (vitamin E) in their femoral pore exudate, which increases the attractiveness of a male's scent to female conspecifics in lacertid lizards (García-Roa et al., 2017; Kopena et al., 2011, 2014). Of all the behaviours we measured, orange morphs performed throat displays more than any other behaviour. Orange males could signal their quality in visual and chemical signals to females, who may choose orange males preferentially over white and yellow males, thus sustaining orange in the population. Additionally, if orange morphs can obtain enough matings via female preference, then orange morphs may not need to expend energy fighting over quality habitat to attract females and persist at lower frequencies in the population. *Podarcis muralis* colour morphs mate assortatively but also engage in considerable heteromorphic matings (Pérez i De Lanuza et al., 2013), suggesting that mate choice patterns may be involved in polymorphism maintenance. Mate choice experiments and behavioural studies that incorporate female morphs are needed to better understand colour polymorphism maintenance in *P. erhardii*.

Conclusions

Colour-polymorphic species have enhanced our understanding of evolution and the maintenance of genetic diversity within species (Svensson, 2017). Here, we showed that male colour morphs in *P. erhardii* differ in their ability to win staged contests over space and in the amount of aggressive, bold, chemosensory and visual signalling behaviours in a neutral arena. Although male colour morphs somewhat differ in head and body size and chemical signal design (Brock et al., 2020) as well as the frequency of different behaviours when in contest with each other over space in a laboratory setting, it is still unclear how exactly these morph-correlated traits are involved in morph fitness outcomes in nature. The cumulative effects of natural and sexual selection likely shape morph genotypes and phenotypes (McKinnon & Pierotti, 2010), morph relative fitness (Sinervo & Lively, 1996; Sinervo & Zamudio, 2001) and morph diversity maintenance within and across populations (Chelini et al., 2021; Corl et al., 2010). To understand what promotes colour morph diversity and coexistence, it will be helpful to know what environmental and ecological factors are associated with morph loss and morph frequencies in populations through time. We also advocate for more research on morph-correlated traits in males and females that explore morph physiology, mating behaviours and mating preferences to determine the nature of morph-specific strategies and the persistence of alternative phenotypes in this species.

Author Contributions

Kinsey M. Brock: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization, Supervision, Project Administration, Funding Acquisition. **Marie-Claire Chelini**: Conceptualization, Formal analysis, Writing – Review & Editing. **Indiana E. Madden**: Investigation, Writing – Review & Editing. **Cynthia Ramos**: Investigation, Writing – Review & Editing. **Cole Ayton**: Investigation, Writing – Review & Editing. **Jessica L. Blois**: Formal analysis, Writing – Review & Editing, Supervision. **Panayiotis Pafilis**: Resources, Writing – Review & Editing. **Danielle L. Edwards**: Conceptualization, Writing – Review & Editing, Supervision.

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Appendix

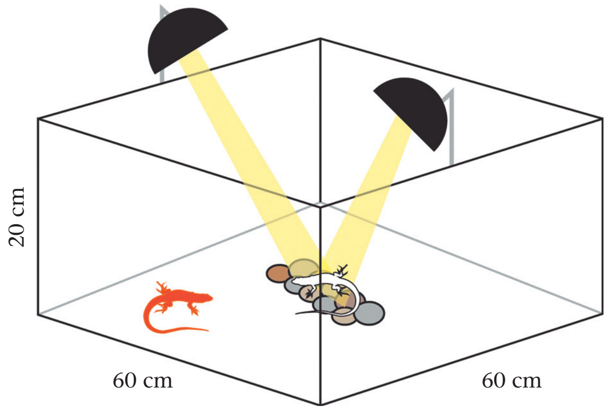

Figure A1. Arena configuration. The experimental arena consisted of a 60 × 60 cm square floor plan with 20 cm high walls. The arena was made out of finished particle board. Finished particle board is easy to sanitize between trials and is opaque, so the lizards would not be disturbed during the trial. We attached two heat lamps to opposite sides of the arena and angled them to shine directly on the stone wall. We created a miniature stone wall out of stones from Moni, the site where we captured all of the lizards. Stones were sanitized between trials.