It ain't easy being orange: lizard colour morphs occupying highly vegetated microhabitats suffer greater ectoparasitism

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Abstract. Intraspecific colour morphs usually differ in more traits than just colour. These traits can manifest as differences in morph physiology, behaviour, and ecology. Ecological differences among colour morphs, such as the degree of parasitism, can influence the evolution, maintenance, and loss of morphs from populations. High ectoparasite load can directly and deleteriously impact host fitness, and thus could influence colour morph persistence in populations if certain morphs are more frequently exposed to parasites or are more susceptible to parasitism. The Aegean wall lizard, *Podarcis erhardii*, is a colour polymorphic island lizard that is parasitized externally by ticks and mites. These ectoparasites can affect aspects of host lizard behaviour and physiology – including thermoregulation and body mass – and therefore are an important factor influencing the ecology and fitness of *P. erhardii*. We find that among sympatric colour morphs, ectoparasite loads differ; namely, monochromatic orange morphs have the highest numbers of ectoparasites, and in general, morphs with orange alleles (orange, orange-white, and orange-yellow) are more heavily parasitized by ticks and mites than the other morphs. Our results indicate that morphs with orange alleles tend to occupy microhabitats with significantly more vegetation cover and thus may increase their exposure to ticks and mites. Ecological differences between morphs could be an important factor contributing to demonstrated patterns of orange morph rarity and loss in *P. erhardii* populations.

Keywords: Aegean islands, colour polymorphism, ectoparasites, lacertid, microhabitat, mite, *Podarcis erhardii*, tick.

Introduction

Colour polymorphic species offer opportunities to explore the causes and consequences of intraspecific phenotypic variation. Present in disparate animal taxa (Gray and McKinnon, 2007; McLean and Stuart-Fox, 2014), and common in lizards (Stuart-Fox et al., 2020), colour polymorphism is the evolution of two or more genetically-determined colour morphs that coexist within a single interbreeding population, the rarest morph too frequent to be explained by recurrent mutation (Huxley, 1955). Colour morphs often differ in other traits besides colour (Stuart-Fox et al., 2020), such as body size (Brock et al., 2020), head

and body shape (Huyghe et al., 2009; Runemark et al., 2010), and behaviour (Sinervo and Lively, 1996; Brock and Madden, 2022), which in turn can influence the relative frequencies of morph genotypes in a population (Sinervo and Lively, 1996). Several colour polymorphic lizard species also have distinct microhabitat use (Pérez i de Lanuza and Carretero, 2018; Brock and Madden, 2022), which can theoretically maintain colour polymorphisms (Chunco, McKinnon and Servedio, 2007). Behaviours linked with space use and habitat segregation could reflect distinct colour morph ecologies (Lattanzio and Miles, 2016). For example, lizard ectoparasites such as ticks and mites vary

in abundance in different habitat types (Bouma et al., 2007; Biaggini, Berti and Corti, 2009). If colour morphs differ in their habitat preference and space use across heterogeneous landscapes, those morph-specific differences might lead to differential exposure to ectoparasites and different parasite loads. Morph differences in ectoparasitism could affect relative morph fitness and frequencies at the population level and result in morph-habitat associations and differences in local morph diversity across the landscape (Pérez i de Lanuza and Carretero, 2018; Brock et al., 2022). Thus, trait differences between intraspecific colour morphs have important ecological and evolutionary ramifications (Sinervo and Lively, 1996; McKinnon and Pierotti, 2010), such as habitat and trophic partitioning (Lattanzio and Miles, 2016; Pérez i de Lanuza and Carretero, 2018) and speciation (Corl et al., 2010).

Lacertid lizards exhibit a high degree of colour polymorphism (Brock, McTavish and Edwards, 2022), particularly in the genus *Podarcis* (Huyghe et al., 2009; Calsbeek, Hasselquist and Clobert, 2010; Runemark et al., 2010; Brock et al., 2020). Colour morphs in several *Podarcis* species have different levels of boldness and aggressive behaviours (Abalos et al., 2016; Brock and Madden, 2022), different levels of activity (Brock et al., 2022a), and partial divergence in habitat use (Pérez i de Lanuza and Carretero, 2018; Brock and Madden, 2022), all of which may influence their exposure to ectoparasites. *Podarcis* lizards are subject to infestation by numerous ectoparasites (Amo, López and Martín, 2005; Foufopoulous et al., 2017), among which ticks and mites are the most common (Amo, López and Martín, 2005; Baeckens and Van Damme, 2018). Specifically, these lizards are most often parasitized by sheep ticks (*Ixodes ricinus*; Bauwens, Strijbosch and Stumpel, 1983; Pafilis et al., 2013) and mites of the genus *Ophionnyssus* (Fain and Bannert, 2000; Garrido and Pérez-Mellado, 2013; Fornberg and Semegen, 2021). Subadult ticks (i.e.,

larvae and nymphs) parasitize lizards by assuming a host-seeking posture called 'questing' (Tälleklint-Eisen and Eisen, 1999), and can wait for days on the tips of grassy vegetation for an opportunity to attach themselves to a passing host to feed on. *Ophionyssus* mites prefer moist dark areas, such as vegetation, to lay eggs (Bannert, Karaca, and Wohltmann, 2000). Once an egg develops into the protonymph stage, mites locate their reptile hosts by smell then lodge themselves under or between scales where skin is accessible before feeding. Thus, the presence of these ectoparasites may be spatially correlated with specific habitat types (Biaggini, Berti and Corti, 2009) where environmental factors such as canopy cover, mat depth of vegetation, and microclimate (i.e., soil moisture, vegetation type, humidity) conditions can influence the prevalence of these ticks (Medlock et al., 2008; Biaggini, Berti and Corti, 2009) and mites (Wu et al., 2019).

The Aegean wall lizard, *Podarcis erhardii*, is a colour polymorphic lacertid lizard that is widely distributed across the Aegean islands and mainland southern Baltics (Valakos et al., 2008; Speybroeck et al., 2016). *P. erhardii* has three discrete monochromatic throat colour morphs (orange, yellow, and white) as well as mosaic combinations (orange-white, white-yellow, and yellow-orange; Brock et al., 2020; Brock et al., 2022b). Both females and males exhibit colour polymorphism and can be any of these six morph types. In males, monochromatic colour morphs differ in head and body size (Brock et al., 2020) and several types of social behaviours including aggression and boldness (Brock et al., 2022a). Specifically, in males, orange morphs have larger heads and bodies and white and yellow morphs tend to be smaller (Brock and Madden, 2022). In males, white and yellow morphs tend to be more bold and active than orange morphs (Brock et al., 2022a). Female colour morphs do not differ in head and body size (Brock et al., 2020), and nothing is currently known about female colour morph social behaviour. Morph

differences in physical and behavioural traits could result in non-overlapping life histories that lead to different space use and thus differential exposure to ectoparasites. Namely, the significantly bolder and more active white morph may move through more habitat, thus increasing its chances of ectoparasite exposure and infestation (Bauwens, Strijbosch and Stumpel, 1983; Salvador et al., 1996; Wu et al., 2019). Infected lizards may have poorer body condition and lower body mass (Megía-Palma et al., 2020), lower social status (Schall and Houle, 1992; Dunlap and Schall, 1995), poorer locomotor performance (Main and Bull, 2000; Garrido and Pérez-Mellado, 2013; but see Ekner-Grzyb et al., 2013), and weaker immune system response (Huyghe et al., 2010). Specifically, increased infestation by ixodid ticks can negatively impact lizard activity and host fitness (Main and Bull, 2000; Heylen and Matthysen, 2008), and increased mite parasitism can result in poorer body condition compared to uninfected lizards (Amo, López, and Martín, 2005). Thus, if certain colour morphs suffer greater rates of ectoparasitism, it could have consequences on relative morph fitness, and thus morph frequencies and maintenance of colour morph variation within populations.

In this study we examine ectoparasite loads in sympatric colour morphs of *P. erhardii* from Naxos island, Greece during the breeding season. Our aim is to determine if ectoparasite infestation differs between colour morphs, and to identify predictors of ectoparasite loads in this species during their peak activity period. We hypothesise that colour morphs will have different ectoparasite loads. Specifically, we expect monochromatic white morphs to have more ectoparasites because they are usually more active and more bold than orange and yellow morphs (Brock and Madden, 2022; Brock et al., 2022a), and thus, potentially move through more habitat increasing their chance of exposure to parasites (Bauwens, Strijbosch and Stumpel, 1983; Salvador et al., 1996; Wu et al., 2019). We also test if morph, sex, and

vegetation cover of an individual's microhabitat are associated with ectoparasite loads in this species. We expect that white morphs, males, and greater vegetation cover are significantly associated with greater ectoparasite loads in this species.

Materials and methods

In June 2019 and 2021 we sampled a total of 600 adult lizards (280 females and 320 males) from the hiking path that connects Moni (37° 4′ 56.7″ N, 25° 29′ 45.2″ E) and Sifones (37° 5′ 50.7″ N, 25° 30′ 47.7″ E) villages on Naxos island in the central Aegean Sea, Greece. This lizard is seasonally active from March – October and exhibits a diurnal daily activity pattern from 0800-1300 and 1600-1800. Lizards were caught from 0800-1300 with a thread lasso attached to the end of a 2.7 m telescopic fishing pole. Upon capture, we measured lizard snout-vent-length (SVL) with Mitutoyo digital precision callipers (Mitutoyo America Corporation, Aurora, Illinois, USA) and only counted ectoparasites on adult lizards with a SVL greater than 45 mm (Valakos et al., 2008; Brock et al., 2020). Two of us visually inspected the throat colour of every lizard and independently assigned lizards to one of six colour morphs, and confirmed that all lizards were independently identified as the same colour morph with no disagreement. One of us counted the number of ticks (*Ixodes ricinus*) and mites (*Ophionyssus* genus) on the surface of the skin using a magnifying glass (fig. 1), starting the examination from the back of the head to the tip of the tail. In this species, ticks are usually found toward the back of the head and upper body, whereas mites are usually clustered behind the legs and in between scales throughout the tail (fig. 1). We noted the sex and colour morph of every individual and released lizards at their point of capture after examination. To avoid recapture of individuals within a year, we marked the left hindleg with a water soluble paint marker. To avoid recapture of measured individuals between years, we only sampled lizards with intact tails in 2021 since all 2019 lizards were tail clipped. This research was approved by the Greek Ministry of Environment (Permits 6ΥΛΥ4653Π8-ΠΞΓ 2019 and ΥΠΕΝ/ΔΔΔ/43912/1357 2021 assigned to K.M. Brock).

To assess the relationship between vegetation cover and ectoparasite loads we conducted vegetation surveys of the microhabitat where lizards were first sighted. Surveys were conducted in a 2 m^2 plot surrounding the exact location each lizard was first observed before capture. On this island, the average home range area in this species is 1.2 m^2 (BeVier, Brock and Foufopoulos, 2021), so our vegetation surveys likely encompass the entire home range. Surveys consisted of using a 1 m^2 collapsible square and estimating the amount of surface area covered by vegetation. Vegetation consisted of grasses (*Avena sterilis*, *Sorghum halepense*), Olive trees (*Olea europea*), bushes (*Pistacea lentiscus*), and dwarf spinose bushes (*Sarcopoterium spinosum*, *Euphorbia*

Figure 1. Tick (A) and mite (B) ectoparasites parasitizing *P. erhardii*. In general, ticks are found dorsally and laterally on the anterior of the lizard. Mites lodge themselves in between scales and usually congregate on the posterior of the body behind the legs and on the tail of the lizard.

acanthothamnos, *Corydothymus capitatus*). Vegetation surveys were performed by the same individual to maintain consistency of estimates and to eliminate observer bias.

To test for morph differences in ectoparasite loads, we pooled tick and mite counts into one ectoparasite count measure (Baeckens and Van Damme, 2018). Because male color morphs have known differences in morphology, performance, and behavior that may influence ectoparasite loads, and females often have fewer ectoparasites than males in many species of lizards (Amo, López and Martín, 2005; Wu et al., 2019), we split our dataset and analysed colour morph differences in ectoparasite loads separately by sex (Baeckens and Van Damme, 2018). We checked the normality of ectoparasite data for females and males with Shapiro-Wilk's tests and assessed homogeneity of variance using Levene's tests. Ectoparasite data were not normally distributed (Shapiro-Wilk's test females: $W = 0.682$, $P < 0.01$; males: $W = 0.519$, $P < 0.01$), nor were variances equal (Levene's test females: $F_{4,275} = 3.457$, $P < 0.01$; males: $F_{5,314} = 10.962$, $P < 0.001$), even after square-root transforming the data. As such, we used non-parametric Kruskal-Wallis tests to determine morph differences in ectoparasite loads. To determine which morphs differed significantly in ectoparasite loads, we used a pairwise Mann-Whitney U test with a Bonferroni continuity correction for multiple comparisons. To test which variables are significant predictors of ectoparasite loads, we used a negative binomial generalised linear model with a log link function. Negative binomial GLMs are appropriate for modelling count data that have excess zeros and or are over-dispersed (Geedipally, Lord and Dhavala, 2012). The model predicting ectoparasite load contained sex, colour morph, and percent vegetation cover of microhabitat as independent variables. We used a One-way ANOVA and post-hoc Tukey HSD test to determine colour morph differences in percent vegetation cover. For all analyses, we designated a statistical significance value *a priori* as alpha = 0.05. All statistical analyses were performed in R Version 4.0.3 (R Core Team, 2021).

Results

Ectoparasite infestation rate for females was 40.4% (113 of 280 individuals) and 65.9%

for males (211 of 320 individuals). Across all colour morphs, males always had more ectoparasites than females of the same colour (table 1).

Female colour morphs differed significantly in number of ectoparasites (Kruskall-Wallis test, $\chi^2_4 = 17.613$, $P < 0.001$). Results from the post-hoc Wilcoxon rank sum test revealed that female orange morphs had significantly more ectoparasites than white morphs (Table 2; Figure 2). Male colour morphs also differed significantly in their ectoparasite loads ($\chi^2_5 = 36.683$, $P < 0.001$). Results from the post-hoc Wilcoxon rank sum test revealed that male orange morphs had significantly more ectoparasites than white, white-yellow, and yellow morphs (table 2, fig. 2). We detected no significant differences among morphs with orange alleles (table 2).

We found that morph, sex, and vegetation cover are significant predictors of lizard ectoparasite loads (table 3). Ectoparasite load increases with increasing vegetation cover (fig. 3a), and morphs with orange alleles were found in microhabitats with more vegetation cover (fig. 3b). Colour morphs differed significantly in the percentage of vegetation cover in their immediate surroundings (ANOVA, $F_{5,594} = 237.81$, $P < 0.001$, fig. 3b). Monochromatic orange morphs were found in microhabitats with significantly more vegetation cover than all other morphs (Tukey HSD, $P < 0.001$, fig. 3b). Morphs with orange alleles (orange-white and yellow-orange) also

Table 1. Mean values and one standard error (SE) of ectoparasites by sex and colour morph. Sample sizes are given for each morph with the exception of orange-white females, which we were unable to find in 2019 and 2021.

Morph	Female Ectoparasite Load Mean ± SE (n)	Male Ectoparasite Load Mean ± SE (n)
orange	21.03 ± 3.05 (60)	47.48 ± 5.01 (60)
orange-white	–	26.05 ± 8.18 (20)
white	7.78 ± 2.35 (60)	17.25 ± 2.35 (60)
white-yellow	11.32 ± 2.59 (60)	15.77 ± 2.70 (60)
yellow	13.62 ± 2.86 (60)	16.00 ± 2.15 (60)
yellow-orange	14.48 ± 3.50 (40)	28.17 ± 3.37 (60)

Table 2. Bonferonni adjusted *P* values from Mann-Whitney U tests on female and male colour morph ectoparasite loads. Orange (OO), orange-white (OW), white (WW), white-yellow (WY), yellow (YY), and yellow-orange (YO) colour morph pairwise comparisons were performed separately for females and males. Statistically significant differences in ectoparasite loads by colour morph and sex are bolded.

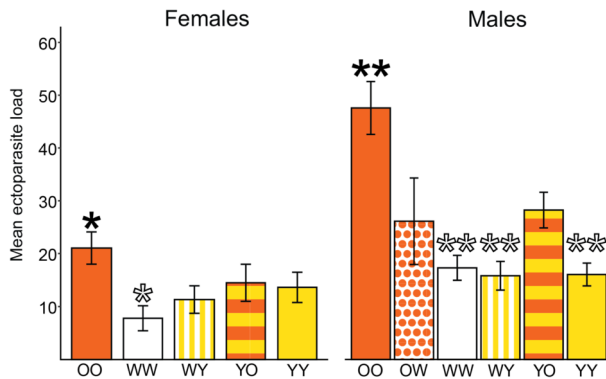|	Females				Males				
Morph	OO	WW	WY	YO	OO	OW	WW	WY	YO
OW	–	–	–	–	0.549	–	–	–	–
WW	**<0.01**	–	–	–	**<0.001**	1	–	–	–
WY	0.067	1	–	–	**<0.001**	1	1	–	–
YO	1	0.086	1	–	0.074	1	0.273	0.079	–
YY	0.279	1	1	1	**<0.001**	1	1	1	0.173

Figure 2. Mean ectoparasite loads and standard error for female and male colour morphs. Significant differences in ectoparasite loads between female colour morphs are noted with single black and white asterisks, and significant differences between male colour morphs are noted with double black and white asterisks. In females, orange morphs had significantly more ectoparasites than white morphs. In males, orange morphs had significantly more ectoparasites than white, white-yellow, and yellow morphs.
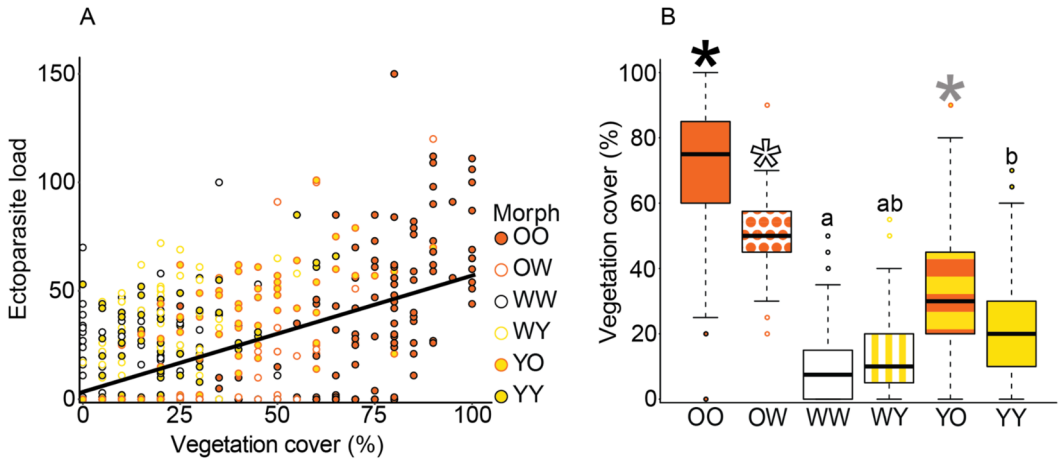
Figure 3. Ectoparasite load has a significant positive relationship with percent vegetation cover (A). Colour morphs differ in percent vegetation cover of their microhabitat (B). Significant differences in vegetation cover (%) are denoted with black, white, and grey asterisks (B). Orange (OO), orange-white (OW), and yellow-orange (YO) significantly differed from each other and all other morphs in the percent vegetation cover of their microhabitat. White morphs (WW) were found in microhabitat with significantly less vegetation cover than yellow (YY) morphs. Neither the white or yellow morph differed from white-yellow (WY) morph in microhabitat vegetation cover.

Table 3. Results from negative binomial generalised linear model of lizard ectoparasite loads. Morph, sex, and percent vegetation cover of an individual's microhabitat are all significant predictors of ectoparasite load. The indicator variable Morph is the expected difference in log count between that morph and the reference morph (Morph: orange).

Ectoparasite load ~ Morph + Sex + Vegetation cover (%)			
Predictor	Estimate	Std. Error	P
Morph: orange-white	0.353	0.049	<0.001
Morph: white	1.499	0.047	<0.001
Morph: white-yellow	1.424	0.045	<0.001
Morph: yellow-orange	0.861	0.031	<0.001
Morph: yellow	1.225	0.040	<0.001
Sex	0.621	0.020	<0.001
Vegetation cover (%)	0.039	0.001	<0.001

had significantly more vegetation cover in their microhabitats than morphs without orange alleles (Tukey HSD, $P < 0.001$, fig. 3b). White morphs were found in microhabitat with the least amount of vegetation cover (fig. 3b). Monochromatic white and yellow morphs differed from each other in percent vegetation cover, but neither differed from white-yellow morphs (Tukey HSD, white-yellow and white difference = 4.75, $P = 0.187$, white-yellow and yellow difference = -5.04, $P = 0.136$, fig. 3b).

Discussion

Intraspecific trait differences among colour morphs can have important ecological and evolutionary consequences (Kusche, Elmer and Meyer, 2015; Stuart-Fox et al., 2020). In this study, we find that ectoparasite loads differ among certain morphs of a colour polymorphic lizard, *Podarcis erhardii*. We predicted that morphs would have different ectoparasite loads, and that monochromatic white male morphs would have the highest ectoparasite loads due to their increased activity and bold behaviours relative to other morphs. Our analyses demonstrate that monochromatic orange morphs have more ectoparasites than other morphs in both sexes. In males, monochromatic orange morphs have significantly more ectoparasites than white, white-yellow, and yellow morphs. In females, monochromatic orange females have significantly more ectoparasites than white morphs. Generally, morphs with orange alleles (orange, orange-white, and yellow-orange) have the highest rates of ectoparastism in both sexes. We also hypothesised that morph, sex, and vegetation cover would predict ectoparasite load in this species, and

our analyses find all three variables to be significant. Ectoparasites impose a fitness cost on their hosts (Combes, 1997; Smallridge and Bull, 2000; Eisen, 2001); therefore, the suite of factors contributing to ectoparasite load differences among colour morphs could play an important role in the maintenance and loss of colour polymorphism in *P. erhardii* populations.

In *P. erhardii*, the proportion of ectoparasite-infested lizards is higher in males than in females, and across the six colour morphs, males consistently maintain larger ectoparasite loads than female morphs of the same colour (table 1). Increased parasitism of male lizards as compared to females has been documented previously in other lizard species (Salvador et al., 1996; Václav, Prokop and Fekiač, 2007; Wu et al., 2019), including those of the genus *Podarcis* (Biaggini, Berti and Corti, 2009). Among male lizards, the effects of elevated levels of testosterone, increased activity levels, and control of larger home ranges may interact to produce the differential parasite infestation often observed between sexes (Salvador et al., 1996; Wieczorek et al., 2020; Barrientos et al., 2021). Additionally, intensity of infection by parasites may fluctuate seasonally for certain sexes (Amo, López, and Martín, 2005; Cox and John-Alder, 2007; Lumbad, Vredevoe, and Taylor, 2011; Tomassone et al., 2017). We conducted our study during the breeding season when testosterone levels are usually at their highest for males (Amo, López, and Martín, 2005; Cox and John-Alder, 2007). High levels of testosterone may lead to greater ectoparasite loads from a combination of increased mating activity-related exposure to ectoparasites (Salvador et al., 1996), and the immunosuppressive effects of testosterone (Oppliger et al., 2004; Amo, López, and Martín, 2005; Cox and John-Alder, 2007; Miles et al., 2007; Fuxjager et al., 2010). Other hormones not closely associated with sex, such as glucocorticoids, can also increase activity (Megía-Palma et al., 2022), and thus, potentially, greater exposure to ectoparasites. An interesting avenue

of future research in this system lies in delineating the relationship between morph mating behaviours, hormone levels, and degree of parasitism.

We find that among males, orange morphs have significantly higher ectoparasite loads than white, white-yellow, and yellow morphs. In general, lizards with orange alleles (orange, orange-white, and orange-yellow) for both sexes are more heavily parasitized by ticks and mites than the other colour morphs in *P. erhardii*. Laboratory contest experiments among monochromatic male colour morphs in this species suggest orange morphs are less active and bold compared to monochromatic white and yellow morphs (Brock and Madden, 2022; Brock et al., 2022a). High parasite loads can inhibit lizard activity (Sorci, Clobert and Michalakis, 1996; Main and Bull, 2000; Bouma et al., 2007), however in the context of *P. erhardii* these findings seem to contradict the premise that higher ectoparasite loads are obtained by high activity and movement over more habitat (Bauwens, Strijbosch and Stumpel, 1983; Salvador et al., 1996; Biaggini, Berti and Corti, 2009; Wu et al., 2019). Yet, the prevalence of ticks and mites is spatially dependent (Bouma et al., 2007) and correlated with specific microhabitat types (Medlock et al., 2008; Wu et al., 2019), which may provide a crucial insight into ectoparasitism discrepancies among *P. erhardii* colour morphs. Indeed, in our study ectoparasite load has a significant positive relationship with microhabitat vegetation (i.e., percent vegetation cover of microhabitat where lizards were observed). Our data show that monochromatic orange morphs occupy the most highly vegetated microhabitats, and that in general, lizards with orange alleles occupy microhabitats with more vegetation cover than the other morphs. Furthermore, *P. erhardii* orange morphs used vegetation more frequently as refuge in simulated predation events in another study (Brock and

Madden, 2022). Consequently, the microhabitat preferences of *P. erhardii* with orange alleles may increase their exposure to parasites if they spend more time in and around vegetation (Pérez i de Lanuza and Carretero, 2018; but see Huyghe et al., 2007). Prevalence of ticks and mites in the environment can vary seasonally (Klukowski, 2004; Lumbad, Vredevoe, and Taylor, 2011; Pollock and John-Alder, 2020), and though we find colour morph differences in ectoparasite loads that are correlated with vegetation cover during the breeding season, determining colour morph exposure to ectoparasites throughout the seasons is worth further exploration. Sex, colour morph, and vegetation cover are all significant predictors of ectoparasite load in this species during the breeding season, and further investigation of morph activity patterns and environmental distributions of ectoparasites and morph ectoparasite loads through the seasons could elucidate in greater detail the ecological and behavioural factors promoting ectoparasite load differences between morphs.

Parasites are broadly considered to adversely affect the fitness of their hosts (Combes, 1997; Smallridge and Bull, 2000; Eisen, 2001). Ectoparasites are vectors to blood parasites (Cooper and Jackson, 1981; Gray, 1991; Smallridge and Bull, 2000; Wu et al., 2019), which together can induce deleterious physiological and behavioural effects for their hosts. In lizards, heavy parasite loads can diminish lizard body condition (Bower et al., 2019; Megía-Palma et al., 2020), locomotor performance (Main and Bull, 2000; Garrido and Pérez-Mellado, 2013; but see Ekner-Grzyb et al., 2013), and immune system response (Huyghe et al., 2010). Body mass has a direct bearing on fighting and mating success in male lizards (Gullberg, Olsson and Tegelström, 1997; Huyghe et al., 2005), while sprinting (i.e., locomotor performance) is important for escaping predation (Hertz, Huey and Garland, 1988; Main and Bull, 2000). Beyond physiological fitness effects, ectoparasites can impact lizard host behaviour (Bower et al., 2019; Megía-Palma

et al., 2020), including home range size (Main and Bull, 2000; Bouma et al., 2007), activity (Sorci, Clobert and Michalakis, 1996; Main and Bull, 2000), and thermoregulation (Megía-Palma et al., 2020). One important aspect of these potential behavioural changes is that they could generate an ectoparasite acquisition positive feedback loop. In the iguanid lizard *Sceloporus occidentalis*, tick-infested lizards seek cooler temperatures in proportion to their tick load (Megía-Palma et al., 2020). If orange *P. erhardii* morphs are predisposed to utilising cooler, highly-vegetated, ectoparasite-dense microhabitats – and primarily acquire ticks through this behaviour – then as their tick load increases, their preference for cooler microhabitat may be reinforced through tick-induced behavioural hypothermia (Megía-Palma et al., 2020). Thus, the orange morphs strong association with cooler, wetter microhabitat may come with the cost of increased ectoparasite exposure. In any case, the relatively high ectoparasite loads sustained by orange morphs could negatively impact orange morph frequencies and the maintenance of colour morph variation within *P. erhardii* populations. Morphs with orange alleles are the least common across every population of this species examined for colour polymorphism (Brock et al., 2022a), and these morphs have gone extinct from almost half of the populations examined in that study. The role of parasitism in population-level morph frequencies and morph extinctions is unknown and worth exploring.

Our study demonstrates that ectoparasite loads differ among sympatric colour morphs of the lacertid lizard *Podarcis erhardii*. Specifically, monochromatic orange morphs harbour the highest numbers of ectoparasites, and in general, lizards with orange alleles (orange, orange-white, and orange-yellow) are more heavily parasitized by ticks and mites than the other morphs. Furthermore, our results indicate that lizards with orange alleles tend to occupy microhabitat with significantly more vegetation cover, which may contribute to these observed

differences in ectoparasite load among morphs. Elucidating any ecological differences between sympatric colour morphs is critical to our understanding of morph dynamics and persistence within and between populations. Parasites can burden lizard hosts with a suite of deleterious physiological and behavioural fitness effects; therefore, in the context of this species, these ectoparasite differences between morphs could be an important factor contributing to demonstrated patterns of orange morph rarity and loss in *P. erhardii* populations (Brock et al., 2022b).

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