

Male throat colour polymorphism is related to differences in space use and in habitat selection in tree lizards

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Abstract

Habitat selection is the disproportionate use of some habitats relative to their availability and is used by animals to maximize fitness. Habitat selection has been the dominant framework for predicting the spatial distribution of animals, but different habitat selection strategies can occur within a population when there are physical or behavioural differences between individuals. Colour polymorphism is often linked to differences in other behavioural and morphological traits, and may therefore affect habitat selection strategy. Male ornate tree lizards (*Urosaurus ornatus*) exhibit a throat colour polymorphism associated with differences in behaviour and in reproductive strategy. Blue-throated males are dominant and defend home ranges containing several females; orange-throated males are either nomadic or sedentary and do not defend territories; and yellow- or green-throated males are reproductive parasites that sneak copulations with females. We tested the hypothesis that throat colour in tree lizards affects habitat selection and space use with mark-recapture data collected from 10 sites in the Chiricahua Mountains of southeastern Arizona, USA. We found that males with green throats moved more than males with blue throats, and that males with orange throats occupied smaller home ranges. Male ornate tree lizards were closer to the highest quality habitat than if their spatial distribution was random, and green-throated males had a more marked preference for the highest quality habitat than blue-throated males. We found no difference in the departures of body temperatures from the preferred body temperature range between males of different throat colours. Survival rates were similar for blue-, green- and orange-throated males. We demonstrated that throat colour polymorphism in ornate tree lizards is related to habitat selection strategy and this may help maintain the colour polymorphism.

Introduction

Habitat selection, the disproportionate use of some habitats relative to their availability (Johnson, 1980) to maximize fitness (Huey, 1991), is one of the most important frameworks for predicting the distribution of animals in space. Organisms can maximize fitness by choosing patches that provide more food resources, lower predation rates and allow organisms to maintain body temperatures to maximize performance (Huey, 1991). The predictive ability of habitat selection was aided by consideration of population density in the Ideal Free Distribution (IFD; Fretwell & Lucas, 1969). The IFD predicts that animals should settle in habitat patches that maximize their fitness based on patch suitability (resources) and the population density in the patch. Despite some unrealistic assumptions (Matsumura, Arlinghaus & Dieckmann, 2010), the IFD has been very powerful for predicting animal distributions between habitats (Milinski, 1979; Walström & Kjellander, 1995; Haché & Bayne, 2013). Importantly, however, the IFD assumes that all

animals in a population exhibit the same behavioural strategy for habitat selection (Morris, 2003).

Alternatively, multiple strategies of habitat selection can occur within a population when there are physical or behavioural differences between individuals. For example, males and females often differ in body size, nutritional requirements and other characteristics that cause optimal habitat selection to differ. Differences in habitat selection strategies between individuals within a population exist in many taxa including birds (Arida & Bildstein, 1997), fish (Ehlinger, 1990), insects (Ahnesjö & Forsman, 2006) and reptiles (Losos *et al.*, 1998). Habitat selection can also be affected by differences in competitive ability, as demonstrated in the Ideal Despotic Distribution (IDD) where dominant individuals monopolize the highest quality habitat (Fretwell, 1972).

Multiple strategies of habitat selection within a population may also occur when species are polymorphic for traits, such as colour, that lead to differences in behaviour. Colour polymorphism is common in many animals (Ford, 1945; Roulin,

2004). The occurrence of within-population colour polymorphism is evolutionarily puzzling because phenotypes with a fitness advantage should become fixed in a population (Gray & McKinnon, 2007). However, within-population colour polymorphism can be maintained by frequency-dependent selection or spatial variation in selection (Roulin, 2004). Frequency-dependent selection maintains colour polymorphism because rare phenotypes have a fitness advantage (Ayala & Campbell, 1974). Spatial variation in selection can maintain polymorphism when the fitness of the phenotypes depends on habitat characteristics (Roulin, 2004; Chunco, McKinnon & Servedio, 2007). Colour polymorphism is often correlated with differences in other traits, such as behaviour and body size (McKinnon & Pierotti, 2010), that affect performance in different habitats (Wunderle, 1981; Munday, Eyre & Jones, 2003). For example, bananaquits (*Coereba flaveola*) occur in discrete black and yellow morphs that prefer shady and sunny nesting and perch locations respectively (Wunderle, 1981). Therefore, differences in habitat selection may be an important mechanism for the maintenance of colour polymorphism (Skúlason & Smith, 1995; Chunco *et al.*, 2007), for instance in several birds (Roulin, 2004) and lizards (Rosenblum, 2006). Thus, testing for differences in habitat selection in polymorphic species can help reveal the role of this particular mechanism in maintaining colour polymorphism.

The ornate tree lizard (*Urosaurus ornatus*) is widespread in western North America and displays a throat colour polymorphism linked to reproductive strategy in males (Moore, Hewst & Knapp, 1998). Males with blue throats are aggressive and defend territories overlapping the home ranges of females (Moore *et al.*, 1998). Orange-throated males can be nomadic or sedentary, depending on resource levels (Moore *et al.*, 1998), and do not defend territories (Moore *et al.*, 1998). Males with yellow or green throats live in between the territories of blue-throated males and sneak copulations with females (Taylor & Lattanzio, 2016). Male throat colour is correlated with differences in aggression (Taylor & Lattanzio, 2016), diet (Lattanzio & Miles, 2016) and microhabitat use (Lattanzio & Miles, 2014). Thus, testing for differences in habitat selection between male throat colour phenotypes will improve our ability to predict space use and will help determine whether habitat selection contributes to the maintenance of the throat colour polymorphism.

We tested the hypothesis that male ornate tree lizard throat colour affects space use and habitat selection because of differences in morphology and behaviour between males of distinct throat colours. We studied habitat selection at a scale where individuals can sample microhabitats, such as variable environmental temperatures, and macrohabitats that occur adjacent to each other. First, we tested whether morphology is correlated with throat colour because these traits are often genetically linked (McKinnon & Pierotti, 2010), and morphology can affect habitat use (Senay, Boisclair & Peres-Neto, 2015). We also tested whether there were differences in survival between males with different throat colours because differences in reproductive strategy or habitat use can affect exposure to predators or other sources of mortality (Sih, 1994). We then tested three predictions derived from our

hypothesis. First, we tested the prediction that blue-throated males should have smaller home ranges and move shorter distances than orange or green-throated males because blue-throated males are territory defenders and the other phenotypes do not defend territories. Second, we tested the prediction that blue-throated males should disproportionately occupy the higher quality habitat that provides a higher fitness benefit (Fretwell & Lucas, 1969) because they are dominant over the other two phenotypes. Third, we tested the prediction that blue-throated males should have smaller deviations of body temperature (T_b) from the species' preferred temperature range (T_{set}) if they occupy higher quality habitat owing to their dominance. Thermal quality is often a strong predictor of habitat selection in ectotherms (Monasterio *et al.*, 2009; Halliday & Blouin-Demers, 2014).

Materials and methods

Study site and species

We studied habitat selection of male ornate tree lizards at 10 sites in the Chiricahua Mountains of southeastern Arizona, USA from 2014 to 2016. Each site straddled a creek bed (wash habitat) and the adjacent wooded area (upland habitat). We studied six sites that were 300 m by 50 m for 3 years (12 capture events). We studied four sites that were 50 m by 50 m for 1 year (two capture events). Ornate tree lizards prefer the wash habitat and the wash has more prey items and allows lizards to achieve T_{set} for a longer period per day than the upland habitat (Paterson & Blouin-Demers, 2018).

During each capture event, we walked through the site at least three times and caught lizards with a noose and pole. We recorded the initial locations of lizards with a handheld GPS unit (fixes were averaged to obtain locations accurate to 1 m). We measured T_b with an infrared thermometer (Pro Point; $\pm 0.1^\circ\text{C}$) placed against the lizard's cloaca (Herczeg *et al.*, 2006; Carretero, 2012). We only measured T_b on lizards that were captured at the exact location where they were detected. We measured the lizards' snout-vent-length (SVL; ± 0.1 mm) and head length (anterior tip of the jaw to the anterior edge of the tympanic aperture on the right side; ± 0.1 mm) with digital callipers, then we gave lizards a unique mark on their ventral side with a medical cauterizer (Ekner *et al.*, 2011) and photographed their ventral side to quantify variation in throat coloration. Since hatchlings emerge in the late summer and reach sexual maturity by the following summer at our study sites (Dunham, 1982), our sample only included adult males.

The throat colour polymorphism in tree lizards is complex (Paterson & Blouin-Demers, 2017). Distinguishing males with discrete throat colours of blue, green and orange based on 10 colour variables is highly accurate based on a Discriminant Function Analysis (97% correct classification; Data S1). Therefore, we divided males into three throat colour categories (blue, green and orange) that are consistent with previous descriptions of throat colour polymorphism in this species (Carpenter, 1995; Lattanzio & Miles, 2014). We assumed the green colour category in our study was equivalent to the

yellow colour category used in previous studies (Lattanzio & Miles, 2014). Since there is significant continuous variation in throat colour (Paterson & Blouin-Demers, 2017), however, we also tested our predictions with the first two principal components of a PCA summarizing 10 colour variables (Data S1). We tested whether the frequency of different throat colour categories changed between years at the six sites monitored for 3 years (Data S1).

Morphology

To test whether lizard throat colour was associated with morphological differences, we used linear mixed-effects models constructed with the R (R Core Team, 2017) package *lme4* (Bates *et al.*, 2015) with each lizard's mean SVL as the response variable. We analysed differences in body size between males with different throat colours using throat colour as a fixed effect and site as a random effect. For all mixed-effects models with significant fixed effects, we compared predicted marginal means with Tukey HSD tests.

We tested for differences in head length between males with different throat colours with linear mixed-effects models. Head morphology in lizards affects prey handling and bite strength (Verwajen, Van Damme & Herrel, 2002), and this can affect resource use and the outcome of competitive interactions. Since head length was strongly correlated with SVL ($F = 716.64$, d.f. = 1, 583, $P < 0.0001$, $R^2 = 0.55$), we included SVL as a covariate in the analyses. Each model included site as a random effect and throat colour as a fixed effect.

Survival

Survival rates of males with different throat colours were estimated for the six sites monitored for 3 years with mark-recapture models in the package *Rmark* (Laake, 2013) to access the program MARK (White & Burnham, 1999) in R (R Core Team, 2017). We did not estimate survival at the other four sites because we only visited each twice. To estimate survival, we used Cormack-Jolly-Seber models (Jolly, 1965; Seber, 1965; Cormack, 1989; Data S1). The probability of observing an individual at a capture event is estimated with parameters for apparent survival (Φ) and detection probability (P). The estimates for Φ were used to compare males with different throat colours.

Mean distance moved

We averaged the linear distance between capture locations for lizards caught at least twice. Lizards were only captured once per survey, so multiple captures for an individual were always separated by more than 1 day. The mean distance travelled did not increase with the number of captures ($F = 0.045$, d.f. = 1, 208, $P = 0.83$, $R^2 < 0.01$). We used linear mixed-effects models to compare the mean distance moved between captures of males with different throat colours. We used the mean distance moved by a lizard as the response variable, throat colour as a fixed effect and site as a random effect.

Habitat selection

To compare the habitat selection of male tree lizards with different throat colours, we used a modification of the distance method (Conner, Smith & Burger, 2003). We calculated the mean coordinates of each individual lizard and measured the minimum distance of the mean coordinates to the wash habitat. Since recaptured lizards did not move far between captures, we believe the mean coordinates of a lizard is a good representation of habitat use in this species. If habitat selection varies between males with different throat colours, then throat colour will affect how close a lizard is to the wash. To test whether male lizards showed a preference for the wash habitat, we compared the distance to the wash of random points generated within the boundaries of each study site to the distance to the wash of the mean coordinates of individual lizards with a *t*-test. We generated 580 random points (the same sample size as the number of male lizards) distributed between the 10 study sites with the *spsample* function in the *sp* package (Bivand, Pebesma & Gomez-Rubio, 2013). We predicted that lizards preferred the wash habitat because the wash has more prey items and allows lizards to achieve their preferred body temperature for a longer period per day than the upland habitat (Paterson & Blouin-Demers, 2018). We believe we quantified habitat selection at an appropriate spatial scale for tree lizards because both habitats are available within the dispersal capabilities of the species. We used linear mixed-effects models to test how throat colour is related to habitat selection using the distance to the wash for a lizard as the response variable, throat colour as a fixed effect and site as a random effect.

Habitat selection can be used to maintain a specific T_b and we tested the prediction that more dominant blue-throated males achieve a T_b closer to T_{set} (32.2–36.0°C; Paterson & Blouin-Demers, 2018) using linear mixed-effects models. We used the accuracy of T_b (d_b), the absolute value of the deviation between T_b and T_{set} (Hertz, Huey & Stevenson, 1993) as the response variable, lizard throat colour as a fixed effect and site as a random effect.

Results

We captured 580 male tree lizards 907 times over three active seasons. Pooling all sites, 81% ($n = 472$) were blue throated, 17% ($n = 99$) were green throated and 1% ($n = 9$) were orange throated. The frequencies of male throat colour categories only differed between years at one site (Table S2, Fig. S2).

Morphology

There was no difference in SVL ($F = 1.29$, d.f. = 2, 594, $P = 0.28$, Fig. 1) or in head length ($F = 1.12$, d.f. = 1, 391, $P = 0.33$) between males with blue (mean SVL 49 ± 1 mm), green (mean SVL 49 ± 3 mm) or orange (mean SVL 49 ± 10 mm) throats. Male SVL was positively correlated with the first ($\beta = 0.2$, $F = 8.97$, d.f. = 1, 491, $P = 0.003$) and negatively correlated with the second ($\beta = -0.3$, $F = 14.62$, d.f. = 1, 497, $P = 0.0001$) principal components of

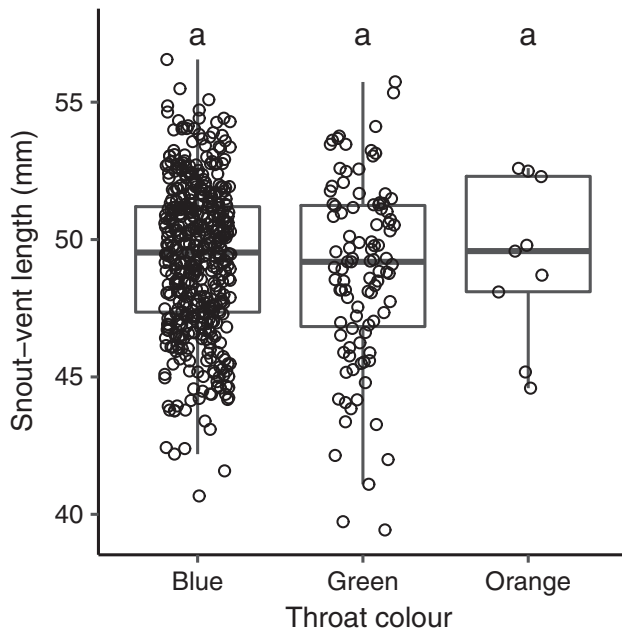


Figure 1 The snout-vent length of male ornate tree lizards (*Urosaurus ornatus*, $n = 580$) did not differ between three categories of throat colour in the Chiricahua Mountains of Arizona, USA.

10 quantitative variables of throat colour (Data S1). However, neither principal components explained much variation in SVL (approximate partial R^2 for first component = 0.02, approximate partial R^2 for second component = 0.03).

Survival

Monthly survival estimates ranged from 0.60 to 0.93, but there were no consistent differences in survival between males with different throat colours (Fig. 2). Orange-throated males were so rare that survival could only be estimated at one site that had more than one individual. The top model for each site did not include differences in survival between throat colours (Tables S4–S9).

Distance moved

The mean distance moved between captures differed between males with different throat colours ($F = 6.8$, d.f. = 2, 203, $P = 0.001$). Orange-throated males moved the least (mean 3.2 ± 1.0 m), blue-throated males moved an intermediate distance (mean 8.4 ± 0.6 m) and green-throated males moved the most (11.4 ± 1.4 m, Fig. 3). Post hoc comparisons indicated significant differences between blue- and green-throated males ($P = 0.006$), and between green- and orange-throated males ($P = 0.006$). The mean distance moved between captures was unrelated to SVL ($F = 0.37$, d.f. = 1, 237, $P = 0.54$).

Habitat selection

Male tree lizards preferred the wash habitat and were on average closer to the wash than random points generated within

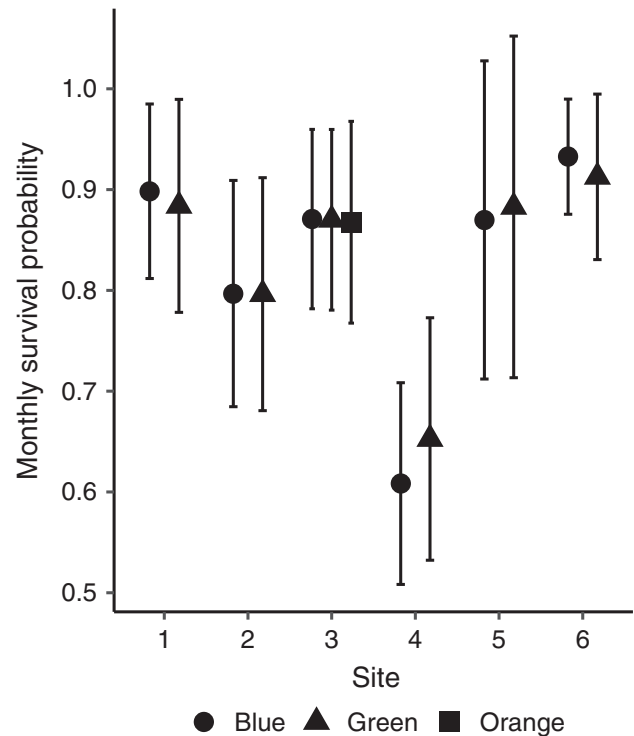


Figure 2 Monthly survival probabilities (\pm SE) of male ornate tree lizards (*Urosaurus ornatus*, $n = 510$) did not differ between three categories of throat colour at six sites in the Chiricahua Mountains of Arizona, USA. Estimates and standard errors are model-averaged from Cormack-Jolly-Seber mark-recapture models. Orange-throated male survival could only be estimated at one site that had more than one individual.

each study site ($t = 6.64$, d.f. = 1125, $P < 0.001$). Males of different throat colour categories differed in their distance to the wash habitat ($F = 3.96$, d.f. = 2, 573, $P = 0.02$). Males with green throats were closer to the wash (mean 8.7 ± 0.9 m) than males with blue throats (mean 12.2 ± 0.6 m, $P = 0.02$, Fig. 4). Males with orange throats were furthest from the wash (mean 14.2 ± 6.2 m), but did not differ significantly from blue-throated ($P = 0.87$) or green-throated ($P = 0.37$) males. The distance to the wash was unrelated to SVL ($F = 0.07$, d.f. = 1, 576, $P = 0.79$). There was no effect of male throat colour on d_b ($F = 0.53$, d.f. = 2, 139, $P = 0.59$, Fig. 5); therefore, throat colour did not affect how close lizard T_b was to T_{set} .

Discussion

Our data partially support the hypothesis that male ornate tree lizard throat colour affects habitat selection. We found evidence that throat colour differences in male ornate tree lizards are related to mean distance moved between captures and to the use of the highest quality habitat. Therefore, differences in habitat selection between colour morphs may help maintain the polymorphism in populations.

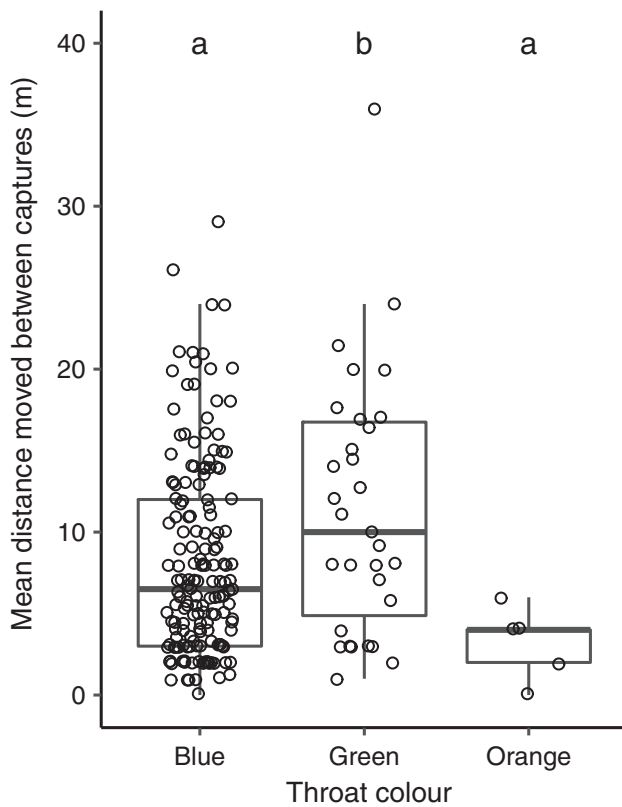


Figure 3 The mean distance moved between captures by male ornate tree lizards (*Urosaurus ornatus*, $n = 209$ lizards recaptured more than once) differed between three categories of throat colour in the Chiricahua Mountains of Arizona, USA.

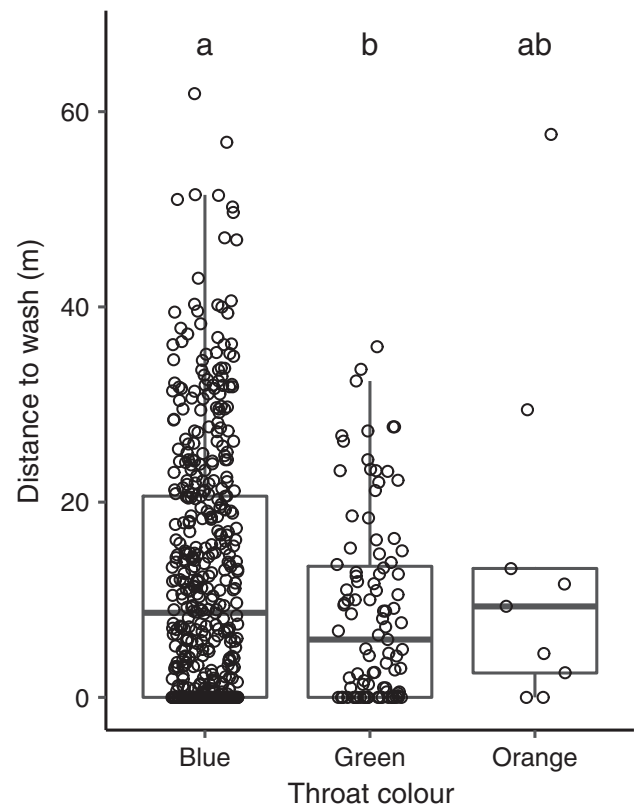


Figure 4 The mean distance to the wash of male ornate tree lizards (*Urosaurus ornatus*, $n = 578$) differed between three categories of throat colour in the Chiricahua Mountains of Arizona, USA.

Male ornate tree lizards with different throat colours overlapped in body size. Thus, differences in habitat selection between males with different throat colours are not driven by differences in body size. However, body size was weakly related to throat colour when colour was treated as a continuous variable. Blueness was positively related to size, consistent with other lizard species (Cox, Zilberman & John-Alder, 2008). In addition, males with more orange on their throats were smaller. However, the continuous variables for throat colour only explained a small amount of variation in male body size, and the relationships may thus not be biologically significant.

There were no differences in survival between males with different throat colours. Blue-throated and green-throated males had similar survival rates at each of the six sites where we could estimate survival. Orange-throated males were rare at all sites and we could only estimate their survival at one site. Different morphs in colour polymorphic species often exhibit differences in survival due to the effect of colour on predation susceptibility (Forsman, 1999). The ornate tree lizard throat colour polymorphism is mostly hidden from visual predators, but differences in behaviour between males with different throat colours may affect survival. Future work should examine

survival at sites where orange-throated males are more common to increase the ability to detect survival differences between colour phenotypes.

We found evidence that throat colour was associated with space use in male tree lizards. Green-throated males moved more than blue-throated males, consistent with the hypothesis that green-throated males exhibit a reproductive parasite strategy and blue-throated males defend small territories (Thompson & Moore, 1991; Lattanzio & Miles, 2014). Orange-throated males moved less than green- or blue-throated males, contrary to the hypothesis that this morph is nomadic (Moore *et al.*, 1998). However, previous studies have found males with orange throats to be nomadic in drought years with low food resources and sedentary in wet years with high food resources (Moore *et al.*, 1998); food may not have been low enough to cause males with orange throats to become nomadic during our study. Again, however, we cannot draw strong conclusions about space use in orange-throated males because they were very rare (nine lizards, or 1% of individuals).

In general, tree lizards prefer the wash habitat (Paterson & Blouin-Demers, 2018). We found evidence that habitat selection differed between throat colour morphs: green-throated males were closer to the wash than blue-throated males. Since population density is higher in the wash habitat than in the

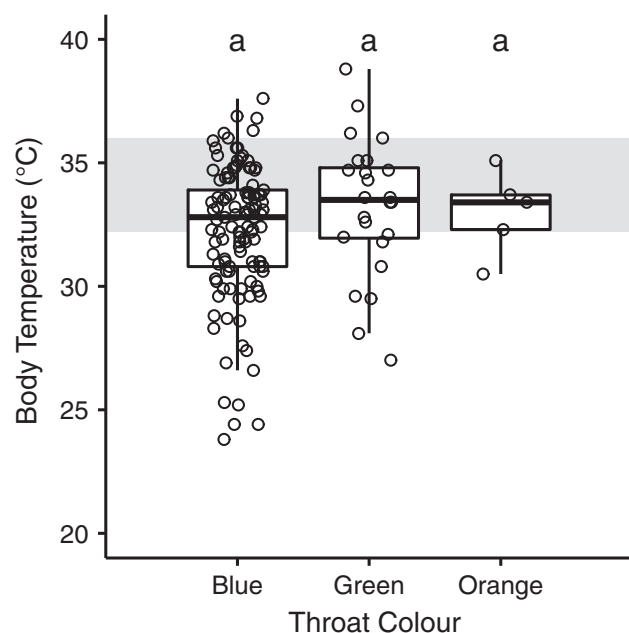


Figure 5 The body temperature of male ornate tree lizards (*Urosaurus ornatus*, $n = 146$) in relation to the species' preferred body temperature (shaded area) did not differ between three categories of throat colour in the Chiricahua Mountains of Arizona, USA.

upland (Paterson & Blouin-Demers, 2018), green-throated males displaying a reproductive parasite strategy (Lattanzio & Miles, 2014) may be more successful in crowded areas where female density is highest. We believe the estimated difference in distance to the wash habitat (5 m) is biologically significant because it is large compared to the mean home-range size (31–70 m²) of males (Zucker, 1989; Mahrt, 1998). However, we did not observe complete segregation of habitat use between morphs, as observed in some polymorphic coral reef fish (Munday *et al.*, 2003).

Ornate tree lizard throat colour did not affect how close lizards were to T_{set} . The majority of T_b measurements (56%) were within the preferred body temperature range of this species (32.2–36°C; Fig. 5) and lizards were close to T_{set} when we caught them (80% of T_b measurements were within 2°C of T_{set}). Therefore, this result may be an artefact of capturing only active individuals, likely engaged in thermoregulation.

Habitat selection based on throat colour can maintain polymorphism within populations. Two commonly proposed mechanisms for the maintenance of polymorphism are frequency-dependent selection (Ford, 1945; Pryke *et al.*, 2007) and niche specialization or partitioning (Skúlason & Smith, 1995). In frequency-dependent selection, a phenotype's fitness depends on the frequency of other phenotypes. For example, the closely related side-blotched lizard (*Uta stansburiana*) exhibits a throat colour polymorphism where three phenotypes are maintained via a rock-paper-scissors game (Sinervo & Lively, 1996). Rare morphs have a fitness advantage and this causes frequencies of

morphs to cycle within populations. Although we only have 3 years of data, the frequencies of different throat colours in male ornate tree lizards did not appear to cycle. The frequencies of throat colour categories only differed between years at one site and we found no evidence of differences in survival between throat colour phenotypes. Side-blotched lizard colour morph frequencies differed every year over 6 years (Sinervo & Lively, 1996), but it is still possible we could not detect changes in frequency between male tree lizard throat colours because our study was too short. Future work on this species could use putative allelic frequencies to try and detect temporal patterns in the polymorphism (Sinervo *et al.*, 2007).

Polymorphism can also be maintained if morphs partition niche axes and pleiotropic effects link colour to behavioural or physiological traits that affect performance in different habitats (Skúlason & Smith, 1995; Roulin, 2004). Our data partially support the hypothesis that male tree lizard throat colour polymorphism affects habitat selection because of differences in behaviour and morphology. Polymorphism was related to differences in habitat selection, but morphs did not differ in morphology. In addition, different throat colours show differences in trophic niche (Lattanzio & Miles, 2016). Thus, the colour polymorphism in male ornate tree lizards may be maintained by niche partitioning between phenotypes rather than by frequency-dependent selection. Future work should further test this hypothesis through experimental manipulations of phenotype frequency, density and habitat. We have made significant progress in identifying the mechanisms that create and maintain colour polymorphisms in different species, such as resource partitioning, frequency-dependent selection and divergent natural selection with gene flow (Gray & McKinnon, 2007). However, the relative frequencies at which these mechanisms operate are still unknown and require further work. Accounting for differences in habitat selection between phenotypes within a population increases our ability to predict the spatial distribution of animals between habitats.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Methods for measuring continuous variation in throat colour, comparing throat colour categories, testing for changes in throat colour frequencies between years, and mark-recapture goodness-of-fit tests for tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of the USA.

Figure S1. The mean snout-vent length (cm) of male ornate tree lizards (*Urosaurus ornatus*, $n = 500$) was positively related to (a) PC1 of throat colour which indicated blueness, and negatively related to (b) PC2 of throat colour which indicated orangeness in the Chiricahua Mountains of Arizona, USA. Black lines are the regression lines and the grey bands are the 95% confidence intervals.

Figure S2. The relative frequencies of three throat colour categories (blue, green and orange) over 3 years in male ornate tree lizards (*Urosaurus ornatus*, $n = 580$) at six sites in the Chiricahua Mountains of Arizona, USA.

Table S1. The variable loadings for PC1 and PC2 in a principal component analysis with 10 variables describing throat colour of male ornate tree lizards (*Urosaurus ornatus*, $n = 720$ photographs of 500 individuals) in the Chiricahua Mountains of Arizona, USA

Table S2. The results of chi-square tests comparing the relative frequencies of three throat colour categories (blue, green and orange) in male ornate tree lizards (*Urosaurus ornatus*) between 3 years at six sites in the Chiricahua Mountains of Arizona, USA

Table S3. Variance inflation estimates (\hat{c}) for general Cormack-Jolly-Seber mark-recapture models at six sites in the Chiricahua Mountains of Arizona, USA for ornate tree lizards (*Urosaurus ornatus*) using bootstrapping (1000 iterations), the median \hat{c} method and Fletcher's \hat{c}

Table S4. Most supported ($< 4 \Delta\text{QAIC}_c$ of most supported model) Cormack-Jolly-Seber models at site 1 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA

Table S5. Most supported ($< 4 \Delta\text{QAIC}_c$ of most supported model) Cormack-Jolly-Seber models at site 2 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA

Table S6. Most supported ($< 4 \Delta\text{QAIC}_c$ of most supported model) Cormack-Jolly-Seber models at site 3 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA

Table S7. Most supported ($< 4 \Delta\text{QAIC}_c$ of most supported model) Cormack-Jolly-Seber models at site 4 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA

Table S8. Most supported ($< 4 \Delta QAIC_c$ of most supported model) Cormack-Jolly-Seber models at site 5 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA

Table S9. Most supported ($< 4 \Delta QAIC_c$ of most supported model) Cormack-Jolly-Seber models at site 6 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA