

Short Notes

Patterns of throat colour variation in *Quedenfeldtia trachyblepharus*, a high-altitude gecko endemic to the High Atlas Mountains of Morocco

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Abstract. The persistence of marked phenotypic variation within species is evolutionarily puzzling. We uncovered remarkable variation in throat colouration in a high-altitude gecko (Atlas Day Gecko, *Quedenfeldtia trachyblepharus*) endemic to the High Atlas Mountains of Morocco. Orange, yellow, and white variants were found in approximately equal proportions in both sexes, and in juveniles and adults. The colour variants did not differ in body size or in body condition, but there was some indication that orange males have relatively longer jaws than white or yellow males. The number of mites harboured by an individual was not a function of its sex or of its throat colouration, but larger lizards did harbour more mites. Our data do not support the hypotheses that throat colour variation is due to selection pressures differing between the sexes or through ontogeny, or signals immunocompetence, but offer some support for the hypothesis that throat colour variation signals dominance. Future investigations on the evolution of throat colour variation in this species should use spectrophotometry to obtain finer colour classification and incorporate measures of fitness.

Keywords: colour polymorphism, natural selection, sexual dichromatism, sexual selection, sexual size dimorphism.

The persistence of marked phenotypic variation within species is evolutionarily puzzling because selection is expected to erode variation with each passing generation. In sexually dimorphic species, however, phenotypic differences between the sexes persist under sexual (Blouin-Demers, Gibbs and Weatherhead, 2005) or sometimes natural selection (Bulté, Irshick and Blouin-Demers, 2008). Notable phenotypic variation can also be the result of mor-

phological or colour changes occurring during ontogeny (e.g., different colouration in adults and juveniles), or during the course of a season (e.g., winter and summer plumage). Genetically-based polymorphisms expressed among adult males or females are rarer and are more puzzling because directional sexual selection or changes in selection pressures through ontogeny cannot be invoked as potential explanations (Gray and McKinnon, 2007). While geographic polymorphisms (Hoekstra, Drumm and Nachman, 2004) can be explained by spatial variation in selection pressures, within population polymorphisms (the existence of distinct, genetically determined morphs within one sex of a breeding population) cannot and, as such, this phenomenon has attracted considerable attention from evolutionary biologists.

Within population polymorphisms could be attributed to random forces such as founder effects, but there is little empirical support

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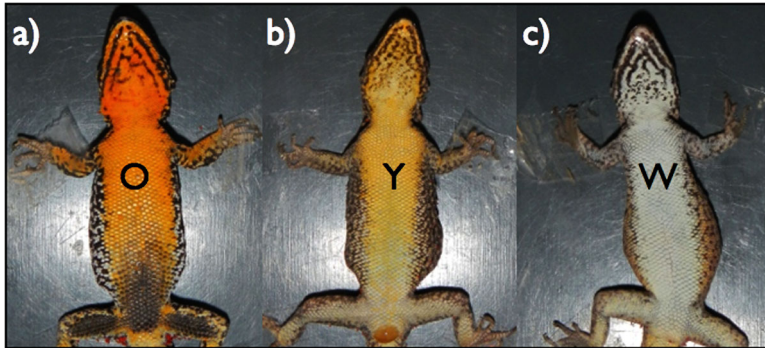


Figure 1. Throat colour variation in *Quedenfeldtia trachyblepharus*, a gecko endemic to the High Atlas Mountains of Morocco: a) is the orange (O) colour variant, b) is the yellow (Y) colour variant, and c) is the white (W) colour variant. Individual a) shows the black pelvic patch that is present in adult males only. This figure is published in colour in the online version.

for random factors being important drivers for the evolution and persistence of morphs (Gray and McKinnon, 2007). Instead, most polymorphisms are attributed to selective forces. In this context, polymorphisms can be transient (one morph has a selective advantage), balanced (the morphs are at a stable equilibrium), or dynamic (the morphs have frequency dependent selective advantage). The coexistence of morphs can be made possible by several mechanisms, such as temporal variation in the form of selection (Calsbeek, Bonvini and Cox, 2010), negative frequency-dependent selection (Sinervo and Lively, 1996; Andrés, Sánchez-Guillén and Cordero Rivera, 2002), apostatic selection (Franks and Oxford, 2011; Calsbeek and Cox, 2012), correlational selection (Brodie, 1992; Lancaster et al., 2007), heterozygote advantage (Penn and Potts, 1999), or morph specific habitat selection (Hedrick, 1993; Chunco, McKinnon and Servedio, 2007).

Lizards feature prominently in the literature on colour polymorphisms. Exceptionally well-studied cases include the rock-paper-scissor game of frequency-dependent selection in *Uta stansburiana* (Sinervo and Lively, 1996) and in *Lacerta vivipara* (Vercken et al., 2007), the temporal fluctuations in selection imposed by predators in *Anolis sagrei* (Calsbeek, Bonvini and Cox, 2010; Calsbeek and Cox, 2012), as well as the intersexual differences in predation

pressures in *Lampropholis delicata* (Forsman and Shine, 1995). Colour polymorphism can also be related to immunocompetence and ectoparasite load in lizards, as was demonstrated in *Podarcis melisellensis* (Huyghe et al., 2010).

We uncovered remarkable variation in throat colouration in a high-altitude gecko (Atlas Day Gecko, *Quedenfeldtia trachyblepharus*) endemic to the High Atlas Mountains of Morocco (fig. 1). Contrary to most geckos that are nocturnal, *Quedenfeldtia trachyblepharus* is strictly diurnal and this may explain why bright throat colours have evolved in this species. We presently do not have pedigree information for this species, so we cannot yet ascertain whether this colour variation is genetically based. Therefore, we refer to colour variants, and not to morphs since morphs have been formally defined as “the coexistence in one interbreeding population of two or more sharply distinct and genetically determined forms, the least abundant of which is present in numbers too great to be due solely to recurrent mutation” (Huxley, 1955). The colour variation in *Quedenfeldtia trachyblepharus* is found within populations, so it cannot be an instance of geographic polymorphism. We collected quantitative data on throat colouration in a single population, but our qualitative observations in neighbouring populations indicate that throat colour polymorphism is not unique to our study population. In a first effort

to uncover the origin of this notable colour variation in *Quedenfeldtia trachyblepharus*, we test predictions arising from four hypotheses.

- Hypothesis 1. Throat colour variation is due to selection pressures (natural or sexual) differing between males and females and is in fact an example of sexual dimorphism. Assuming that throat colour variation is not neutral in one sex, differing selection pressures between the sexes would select for different colour variants in males and females. The presence of different colour variants or differences in variant frequency between sexes would support this hypothesis.
- Hypothesis 2. Throat colour variation is due to selection pressures (natural or sexual) differing through ontogeny. Assuming that throat colour variation is not neutral in one life stage, differing selection pressures through ontogeny would select for different colour variants at different life stages. The presence of specific colour variants at given life stages would support this hypothesis.
- Hypothesis 3. Throat colour variation signals dominance, as is the case in the frequency-dependent rock-paper-scissor game of *Uta stansburiana* (Sinervo and Lively, 1996). If individuals of certain colour variants are larger, have longer jaws, or are in better body condition, this would be consistent with this hypothesis, assuming that size, jaw length, and condition are important determinants of dominance, as has been shown in other lizards (Salvador et al., 2008; Husak et al., 2009).
- Hypothesis 4. Throat colour variation signals immunocompetence (Huyghe et al., 2010). If individuals of certain colour variants harbour more ectoparasites, this would be consistent with this hypothesis, assuming that the number of ectoparasites is related to immunocompetence.

Over 4 days in June 2012, we captured 213 *Quedenfeldtia trachyblepharus* (106 males, 92 females, and 15 juve-

niles) in a 2.5-ha study plot at Oukaïmeden in the High Atlas of Morocco (2600 m). We brought the lizards back to a field laboratory and took digital photographs (Nikon Coolpix AW100) of the ventral surface of each individual under standardized conditions: flash photography, indoor lighting, same grey background, equal distance. Then, we measured snout-vent length (SVL) and tail length (± 1 mm) by juxtaposing the lizards against a ruler, and mass with an electronic balance (± 0.001 g). We measured jaw length on the left side of the head with digital calipers (± 0.1 mm). We determined sex based on the presence of cloacal swellings. We enumerated the number of mites attached to the body of each individual. All geckos received a dot of paint on the dorsal surface (to prevent recapture) and were released at their location of capture the following day.

Upon returning from the field, we asked an independent observer (CV) to score the dominant background throat colouration of each individual as orange (O), yellow (Y), or white (W) based on the digital photographs. We asked two other independent observers to score throat colour and their scores were the same in $>95\%$ of cases. The few discrepancies were between orange and yellow. We did not find intermediate colour variants. We obtained an index of male body condition by calculating the residuals from a linear regression of log mass on log SVL. We excluded all females from body condition calculations because of variation in their reproductive status (some gravid, some having just laid eggs). We also excluded 4 males for which the tail represented less than 80% of SVL, indicating an incompletely regenerated tail that would affect mass measurements. We denote independent variables as X and dependant variables as Y. We ran fully factorial models, but we only present interaction tests when they were significant. All analyses were conducted on JMP 10.0 (SAS Institute, Cary, North Carolina).

Hypothesis 1: sexual dimorphism. The 106 adult males (mean SVL \pm SE = 46.2 ± 0.2 mm) were, on average, 7.3% larger than the 92 adult females (42.8 ± 0.2 mm) and this difference was statistically significant (ANOVA; X = sex; Y = SVL: $R^2 = 0.47$, $F_{1,196} = 174.2$, $p < 0.001$). Controlling for differences in SVL, adult males (least-square mean jaw length \pm SE = 11.95 ± 0.05 mm) also had, on average, 6.8% longer jaws than adult females (11.14 ± 0.05 mm) and this difference was statistically significant (ANCOVA; X = sex, SVL, sex * SVL; Y = jaw length: partial R^2 of sex = 0.15, $F_{1,179} = 125.6$, $p < 0.001$). In addition, all 106 adult males, but none of the 92 adult females or 15 juveniles, exhibited a black pelvic patch (fig. 1a), suggesting that this black pelvic patch appears at sexual maturity in males only. Thus, there appears to be sexual dichromatism, combined with clear sexual size dimorphism in both

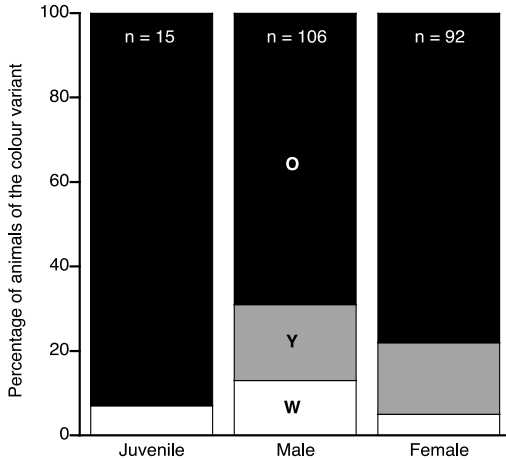


Figure 2. Frequency of the orange (O), yellow (Y), and white (W) throat colour variants in 15 juvenile, 106 male, and 92 female *Quedenfeldtia trachyblepharus*, a gecko endemic to the High Atlas Mountains of Morocco.

body size and proportional jaw length, in *Quedenfeldtia trachyblepharus*.

All three colour variants were present in adult males and adult females, with the orange variant being more prevalent than the white and yellow ones (fig. 2). Among adults, the orange colour variant was more frequent, and the white colour variant was less frequent, in females than in males, but the difference was only marginally significant (contingency table analysis; $X = \text{sex}$; $Y = \text{colour}$: $\chi^2_2 = 5.16$, $p = 0.076$).

Hypothesis 2: ontogeny. We only detected the orange and white variants in the 15 juveniles and, therefore, there was a marginally significant difference in the proportion of the three colour variants between juveniles and adults (contingency table analysis; $X = \text{life stage}$; $Y = \text{colour}$: $\chi^2_2 = 5.92$, $p = 0.052$). This marginally significant difference could be due to our smaller sample of juveniles than of adults. In fact, if the yellow variant had the same frequency among juveniles than among adults (ca. 18%), we should have detected fewer than 3 in our sample of 15 juveniles. Thus, it is possible that the yellow variant is present in juveniles, but that we failed to detect it.

Hypothesis 3: dominance. For these analyses, we excluded the small sample of 15 juveniles

for which we could not determine the sex. Controlling for the effect of sex on body size, individuals of the three colour variants were the same size (ANOVA; $X = \text{sex}$, colour, sex * colour; $Y = \text{SVL}$: partial R^2 of colour = 0.01, $F_{2,192} = 1.15$, $p = 0.319$). Controlling for the effect of body size and sex on jaw length, individuals of the three colour variants had jaws of the same size (ANCOVA; $X = \text{SVL}$, sex, colour, SVL * sex, SVL * colour, sex * colour, SVL * sex * colour; $Y = \text{jaw length}$: partial R^2 of colour = 0.01, $F_{2,186} = 1.55$, $p = 0.214$), but there was one marginally significant interaction (partial R^2 of sex * colour = 0.01, $F_{2,186} = 2.41$, $p = 0.092$). Controlling for the effect of body size on jaw length, females of the three colour variants had jaws of the same size (ANCOVA; $X = \text{SVL}$, colour, SVL * colour; $Y = \text{jaw length}$: partial R^2 of colour = 0.01, $F_{2,86} = 0.63$, $p = 0.535$). On the other hand, controlling for the effect of body size on jaw length, males of the three colour variants differed in jaw length (ANCOVA; $X = \text{SVL}$, colour, SVL * colour; $Y = \text{jaw length}$: partial R^2 of colour = 0.05, $F_{2,100} = 3.97$, $p = 0.022$). Orange males (least-square mean jaw length \pm SE = 12.22 ± 0.04 mm) had jaws that were 1.5% larger than white males (12.05 ± 0.10 mm) and 2.0% larger than yellow males (11.97 ± 0.08 mm). Finally, males of the three colour variants did not differ in body condition (ANOVA; $X = \text{colour}$; $Y = \text{condition}$: partial R^2 of colour = 0.02, $F_{2,99} = 1.22$, $p = 0.300$).

Hypothesis 4: immunocompetence. Lizards harboured a mean of 26.2 ± 1.6 mites (range 0 to 114), but the number of mites harboured by an individual (log transformed) was not related to its sex (ANCOVA; $X = \text{sex}$, colour, SVL, sex * colour, sex * SVL, colour * SVL, sex * colour * SVL; $Y = \log \text{mites}$: partial R^2 of sex = 0.01, $F_{1,186} = 0.92$, $p = 0.338$) or to its throat colouration (partial R^2 of throat colour = 0.02, $F_{2,186} = 0.39$, $p = 0.675$), but larger individuals had more mites than smaller individuals (partial R^2 of SVL = 0.03, $F_{2,186} = 5.83$, $p = 0.017$).

Despite clear sexual size dimorphism, we found the same orange, yellow, and white throat colour variants in male and female *Quedenfeldtia trachyblepharus* with approximately equal proportions, albeit there was a marginally significant tendency to have more white variants and fewer orange variants among males than among females. In addition, orange and white variants were present in juveniles. Because our sample of juveniles was modest, it seems plausible that we may have failed to detect one of the rare colour variants (yellow) for this age class. Thus, it appears that all three colour variants may be present throughout ontogeny, and it is clear that all three colour variants are present in males and females. Therefore, these data do not support the hypotheses that throat colour variation is due to selection pressures (natural or sexual) differing between the sexes or that throat colour variation is due to selection pressures differing through ontogeny, unless throat colour is sometimes selectively neutral (for instance, during part of ontogeny or in one sex).

Individuals of the orange, yellow, and white throat colour variants did not differ in body size and, among males, did not differ in body condition. There was some indication, however, that orange males had relatively longer jaws than white or yellow males, but the size difference in relative jaw length was small (2%, much less than the 7% difference between males and females). In addition, if advertising dominance were a key function of throat colour, we would have expected differences between all three colour variants. In some lizards, males with proportionally larger jaws bite harder, and therefore sire more offspring (Husak et al., 2009). Therefore, these data partially support the hypothesis that colour variation could signal dominance, but the evolutionary significance of the small difference in relative jaw length remains unresolved.

Individuals of the three throat colour variants did not differ in their parasite loads, even though geckos harboured a lot of mites and if larger individuals harboured more mites than smaller in-

dividuals. Therefore, these data do not support the hypothesis that throat colour variation signals immunocompetence.

One important caveat that we must make in relation to our study is that we did not have any direct measures of fitness, and our conclusion should thus be considered tentative. A firmer conclusion will need to await data on how the three colour variants differ in fitness (clutch size, reproductive rate, survival, etc.) and on more refined measures of dominance and immunocompetence. Data on the relationship between relative jaw length in males and reproductive success would be especially enlightening.

So what could maintain throat colour variation within populations of *Quedenfeldtia trachyblepharus*, in addition to its potential role in signalling dominance? There are several possibilities, but it appears that temporal variation in selection or frequency dependent selection are the most likely explanations given their proven role in other lizard species (Sinervo and Lively, 1996; Calsbeek, Bonvini and Cox, 2010). Determining which explanation is correct will require estimating selection gradients on each colour variant and how these selection gradients vary through time. As a first step, future investigations on the evolution of throat colour variation in this species should use spectrophotometry to obtain finer colour classification and determine with certainty whether this variation represents a discrete or a quantitative trait. Some lizards where a discrete polymorphism was inferred (Vercken et al., 2007) were later shown to exhibit gradual variation (Côté et al., 2008). Pedigree information would also help confirm whether the colour variants represent a true polymorphism *sensu stricto* (Huxley, 1955) or phenotypic plasticity. In addition, documenting the inter-population variability in colour variant composition and its stability through time would be valuable to infer whether spatial or temporal variation in selection is contributing to colour variation. Finally, our finding that the black pelvic patch is only found in mature males

is intriguing and its functional significance deserves further study.

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