Polymorphism, parallel evolution, and purpose of dewlap hue in Lesser Antillean *Dactyloa* anoles

Roger S. Thorpe[1*], Helena Johansson[2], Yann Surget-Groba[3] and Jacqueline A. Thorpe[4]

[1] Molecular Ecology and Evolution at Bangor (MEEB), School of Natural Sciences, Bangor University, LL57 2UW, UK.

* Corresponding author (r.s.thorpe@bangor.ac.uk)

[2] Natural Resources Institute Finland (Luke), Latokartanonkaari 9 00790 Helsinki, Finland.

[3] Institut des Sciences de la Foret Temperee, Universite du Quebec en Outaouais, 58 rue Principale, Ripon, QC J0V 1V0, Canada.

[4] Contact R. S. Thorpe

Edited by: S. Blair Hedges. **Date of publication**: 26 September 2024.
Citation: Thorpe RS, Johansson H, Groba YS, Thorpe JA (2024). Polymorphism, parallel evolution, and purpose of dewlap hue in Lesser Antillean *Dactyloa* anoles. *Caribbean Herpetology* 96: 1–13.
DOI: https: //doi.org/10.31611/ch.96

Abstract

Against a background of conservative dewlap hue among Lesser Antillean *Dactyloa* anoles, within-population polymorphism is present in a Martinique habitat where UV/grey dewlaps are markedly different to the widespread yellow/orange dewlaps. Moreover, parallel evolution on Martinique and St. Vincent of 1) UV/grey dewlaps in similar habitats, and 2) small but consistent differences between dewlap hue in xeric versus montane habitats, imply natural selection. Anole dewlaps are widely thought to have a role in species recognition and potentially act as a pre-mating isolating mechanism, and this is compatible with the degree of genetic isolation in an "ecological speciation" paradigm, but not in an "allopatric speciation" paradigm.

Keywords: anole, *Dactyloa*, Lesser Antilles, dewlap, spectrometry, ultraviolet markings, parallel evolution, speciation, isolating mechanisms.

Introduction

Anoles are a speciose group of small, insectivorous, largely arboreal, lizards occupying the New World. Males have an enlarged dewlap that can be used for intraspecific signalling as well as other purposes (Losos 2009). Geographic variation in dewlap hue within a species has been investigated in a few Lesser Antillean species and, for example, *Ctenonotus* (formerly *Anolis*) *distichus* (Losos 2009, Glor & Laport 2012) and *Ctenonotus (Anolis) cristatellus* (Leal & Fleishman 2004) from the Greater Antilles. While geographic variation has been found in dewlap hue, wide ranging within-deme polymorphism is unreported, and few studies have used reflectance spectrometry to characterize intraspecific within-island dewlap hue in anoles to test for natural selection and its role as a pre-mating isolating mechanism. This study investigates geographic variation in dewlap hue in two southern Lesser Antillean anole species in the genus *Dactyloa* (previously in *Anolis*) using reflectance spectrometry in order to investigate parallel evolutionary adaptation to habitats, reveal and quantify dewlap polymorphism in a region, and reveal whether dewlap hue variation is compatible with allopatric and/or ecological speciation.

These two species, *Dactyloa trinitatis* from St. Vincent and *D. roquet* (a complex) from Martinique, are both medium sized generalists found across most of their respective islands and show pronounced geographic variation in dewlap hue and other quantitative traits corresponding to the various habitats within them (Thorpe 2002, 2022; Thorpe and Stenson 2003; Thorpe *et al.* 2015). These species are not sister taxa (Thorpe *et al.* 2018) and are comparable even though *D. roquet* is solitary and *D. trinitatis* has a single sympatric congener. Both St. Vincent and Martinique have pronounced climatic and vegetational zonation within them such that some areas, particularly the Caribbean coast in the rain-shadow, are xeric, the higher elevations have montane rainforest, and the Atlantic coast may have evergreen littoral woodland (Malhotra 2022). These two species both show dewlap hue differences between xeric and montane rainforest habitats, and both can be seen to show UV/grey dewlap in Atlantic littoral woodland habitats.

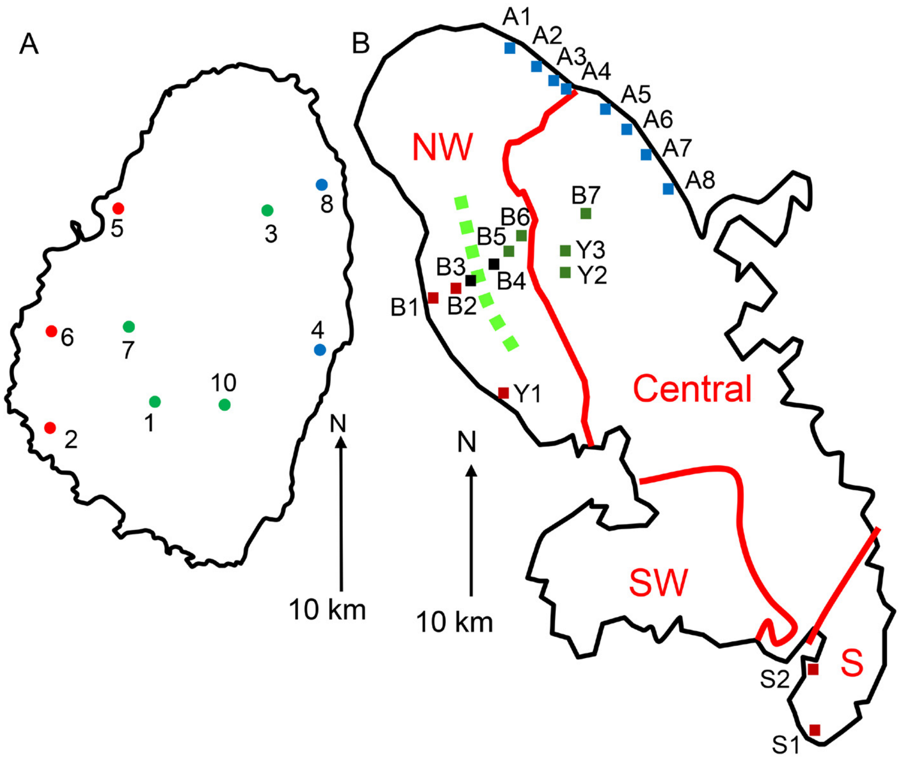

Figure 1. Map showing the localities. **(A)** *Dactyloa trinitatis* on St. Vincent. Xeric, montane and evergreen littoral habitats are red, green and blue respectively. See Thorpe (2002) and Thorpe *et al.* (2015). **(B)** *Dactyloa roquet* complex on Martinique. In the NE, transect A localities on the Atlantic coast are blue, while elsewhere for the xeric versus montane contrast, xeric localities are in red and montane are in green (while black localities are unassigned). For transects and localities labelled A, B and S see Thorpe *et al.* (2010) transects I, IV and VII respectively, and for localities labelled Y see Surget-Groba *et al.* (2012). The broken light green line indicates an ecotone while the red lines indicates the distribution of lineages (NW=northwest, Central, SW=southwest and S=south) from precursor island (Thorpe *et al.* 2010).

The islands are, however, not identical. St. Vincent (Fig. 1a) is a typical mountainous, lozenge-shaped, younger island, thought to be around 3.5 my old (Maury *et al.* 1990). It has the relatively simple, marked climate and habitat zonation associated with elevation, typical of such montane Lesser Antillean islands (Thorpe 2022). The western coastal extremity and southern tip are xeric with thorny scrub and deciduous or semideciduous trees and with annual precipitation under 2000 m (Thorpe 2002, 2022). There is montane rainforest at 300-500 m elevation, with lower temperatures and much higher annual rainfall (Thorpe 2022). The Atlantic littoral woodland is evergreen, generally more mesic than the xeric woodland in the rain-shadow on the Caribbean coast and may be sculpted by the prevailing winds (Malhotra 2022). St. Vincent remains volcanically active, but recordings used in this study were collected prior to the April 2021 eruption in the north of the island.

Martinique (Fig. 1b), on the other hand, is a much more geologically complex island being composed of older and younger arc precursor components. These precursor islands are thought to have joined to form the current island of Martinique relatively recently as described in Thorpe *et al.* (2008, 2010), Surget-Groba *et al.* (2013), and Thorpe (2022). Similar to St. Vincent and other montane islands in this archipelago, the Caribbean coastal strip in the rain-shadow of the northern mountains, and the far south, are xeric and while the slopes of the northern mountains are cooler and wetter with montane rainforest (Thorpe 2022). In the north, the change from xeric to montane rainforest habitat is quite sharp (Ogden and Thorpe 2002; Thorpe *et al.* 2008, 2010). The northern Atlantic coast at the latitude of these mountains has Atlantic littoral woodland, but in the far north this becomes more mesic, and the tip of the eastern peninsula and some small eastern islets are more xeric (Thorpe 2022). As well as showing parallel habitat variation to St. Vincent, the sharp ecotones between habitats (xeric versus montane) and secondary contact between anole populations on the precursor islands, also allows the variation in dewlap hue to be compared to ecological and allopatric speciation patterns.

A series of studies of *Dactyloa roquet* has investigated the gene flow and genetic isolation along transects (Ogden and Thorpe 2002; Thorpe *et al.* 2008, 2010; Surget-Groba *et al.* 2012; Johansson *et al.* 2008) in relation to habitat and precursor islands. These studies show a genetic structure that conforms to both allopatric and ecological models of speciation in different transects. Where the central precursor island meets the north-west precursor island on the NE coast (Fig. 1b, transect A) there is a dramatic switch from central to NW lineage and a reduction in genetic exchange (characterized by microsatellites) that is compatible with an allopatric model of speciation: the populations having diverged on these precursor islands while geographically isolated (transect I in Thorpe *et al*. [2010]). In contrast, an ecological model of speciation predicts increased genetic isolation between the populations in the xeric habitat with those in the montane habitat, and this is seen in the genetic structure along transect B in Fig. 1b (transect IV in Thorpe *et al.* [2010]). The precursor islands do not contact at this point, nor is there any switch in anole lineage.

Methods

Sampling procedure. Reflectance spectrometry recordings in this study were taken from two previous independent studies with different aims and sampling regimes. The previous study of *D. trinitatis* on St. Vincent was based on an island-wide description of the dewlap hue (Thorpe 2002). For the current study this allowed the selection of sites from xeric, montane and Atlantic littoral habitats to be used to compare dewlap hue in different habitats (Fig. 1a). The previous study of the *D. roquet* complex on Martinique (Thorpe *et al.* 2010) was based on a series of multiple site transects across ecotones and secondary contact zones to investigate allopatric and ecological speciation. For the current study this allowed both, 1) the selection of transects to compare dewlap hue in relation to these two speciation paradigms and also, 2) the selection of replicate sites from the various transects to compare the dewlap hue in different habitats (xeric, montane and Atlantic littoral) (Fig. 1b). The latter allowing this study to reveal parallels, in dewlap hue variation in relation to habitat, between these two species, *D. trinitatis* and *D. roquet*.

Reflectance spectrometry. For *D. trinitatis* from St. Vincent, reflectance spectrometry was performed with four repeat measures on 5–8 males per locality using the procedure in Thorpe (2002). Localities were selected to represent replicates of different habitat types (xeric, montane rainforest and littoral Atlantic) (Fig.1a). For *D. roquet* from Martinique reflectance spectrometry was performed with at least three repeat measures on around ten individuals per locality (Fig. 1b) using the procedure in Thorpe *et al.* (2008, 2010).

For both species, reflectance was recorded in the laboratory, measuring the centre of the dewlap disc, from 330 nm to 710 nm and then averaged across repeat measurements for each individual. In this study, scores for each individual were subsequently analysed in 20 nm segments and expressed as the percentage of the total area under the reflectance curve occupied by each of these 19 segments. This approach discards information about total intensity. Data were analysed using custom-written Fortan programs and Excel. For *D. trinitatis* standard RGB images of the dewlap were compared to UV-reflectance-only images using the photographic method in

Thorpe & Richard (2001).

Polymorphism test. The graphs of reflectance against wavelength for each recording for each individual were visually scanned. In one region the differences between the various repeat measurements per individual were consistent but between-individual differences were pronounced suggesting two morphs per locality. In these localities we characterized the two types of spectrometry profiles by comparing lower wavelength reflectance (segment 7, 430–450 nm) with higher wavelength reflectance (segment 19, 690–710 nm). To give a positive score for this wavelength discriminator the higher wavelength score was subtracted from an arbitrary constant (12) and the product added to the lower wavelength score such that "yellow/orange dewlaps" had a low score, and "UV/grey dewlaps" had a high score. This wavelength discriminator was then figured as a histogram with 25 bins. Further, these reflectance curves were illustrated as reflectance versus wavelength graphs. Data were analysed using Excel.

Atlantic littoral habitat: Martinique—*D. roquet*. The frequency of two different morphs of dewlap (based on the wavelength discriminator) were plotted along the transect A1 to A8 (Fig. 1b) on the Atlantic coast which gradually goes from a more mesic habitat in the north to an Atlantic littoral habitat further south. The mean of each morph (pooled across all 8 localities) for each of the 19 wavelength segments was compared using "t" tests in SPSS with a Bonferroni corrected significance threshold of $P \leq 0.0026$ (i.e. 0.05/19).

Atlantic littoral habitat: St Vincent—*D. trinitatis*. The dewlap hue at two Atlantic littoral habitat localities (4, 8) were compared to the seven remaining localities (xeric plus montane - 1, 2, 3, 5, 6, 7, 10) (Fig.1a) using contrast ANOVA. This was repeated across the 19 wavelength segments in SPSS using a Bonferroni corrected significance threshold of $P \leq 0.0026$.

Xeric versus montane habitats: St Vincent—*D. trinitatis*. The dewlap hue at the three xeric localities (2, 5, 6) were compared to the four montane localities (1, 3, 7, 10) (Fig. 1a). Dewlap hue in these two habitat sets were compared across the 19 wavelength segments using contrast ANOVA as above.

Xeric versus montane habitats: Martinique—*D. roquet*. To compare dewlap hue in xeric and mesic habitats five xeric localities (B1, B2, S1, S2, Y1) were selected and compared to five selected montane localities (B5, B6, B7, Y2, Y3) (Fig. 1b). These two habitat sets were compared using contrast ANOVA as above.

Dewlap hue and allopatric model of allopatric speciation. Thorpe *et al.* (2010) has demonstrated that the genetic structure along transect A conforms to an allopatric model of speciation between the NW lineage (A1, A2, A3, A4) and central lineage (A5, A6, A7 A8). The frequency of the above two dewlap morphs found along transect A were plotted in comparison to the precursor islands, lineages and genetic structure taken from transect IV in Thorpe *et al.* (2010) to reveal if the frequency of the dewlap morphs is related to the expectations of allopatric speciation.

Dewlap hue and the model of ecological speciation. Thorpe *et al*. (2010) has demonstrated that the genetic structure along transect B conforms to an ecological model of speciation. A canonical variate analysis was carried out on the seven localities (groups) across the 19 wavelength segments (characters) for transect B using SPSS v27. Locality mean canonical variate 1 (CV1), expressing dewlap hue, was then plotted along transect B in comparison to the habitat type and genetic structure taken from transect IV in Thorpe *et al.* (2010) to indicate if dewlap hue is compatible with the expectations of ecological speciation. Moreover, a contrast ANOVA was run on CV1 to compare dewlap hue from the either side of the ecotone between the xeric (B1, B2, B3) and montane (B4, B5, B6, B7) habitats.

Results

Transect A bimodality for *D. roquet*. The histogram in Fig. 2 suggests that dewlap hue is bimodal for *D. roquet* at the localities in transect A. Examples from this transect (Fig. 3a) show that the typical dewlap morph in the yellow/orange range has low reflectance at low wavelengths and a sharp rise to the yellow/orange range, while the UV/

grey dewlap morph has relatively high reflectance in low wavelengths which rise modestly and more gradually at the higher wavelengths. When the mean reflectance is compared between these morphs for each wavelength segment then the UV/grey morph has significantly higher reflectance from the 330+ segment to the 510+ segment while the yellow/orange morph has significantly higher reflectance from the 530+ to 690+ segments (Table 1). The examples of dewlap morphs in Fig. 3a are imaged in Fig. 4 showing the rather dull, non-focal, UV/grey dewlap contrasting with the more saturated dewlap in the yellow to orange range.

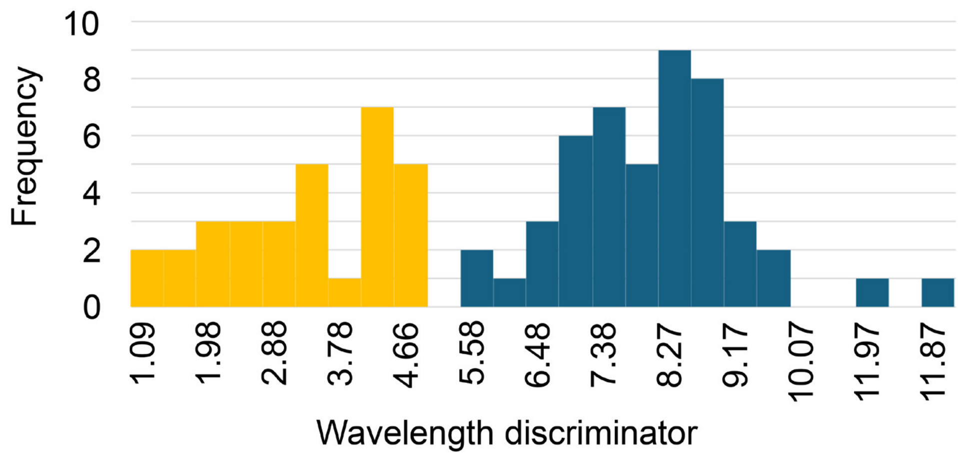

Figure 2. Histogram of the frequency of dewlap spectrometry profile for the 79 individuals along transect A, NW Martinique, using the wavelength discriminator described in the "polymorphism test" in the text. The individuals with spectrometry profile showing the typical orange/yellow dewlap (N = 31) are coded in orange and those with the atypical UV/grey dewlap (N = 48) are shown in blue. Both morphs are present at all sites along transect A (Fig. 1b).

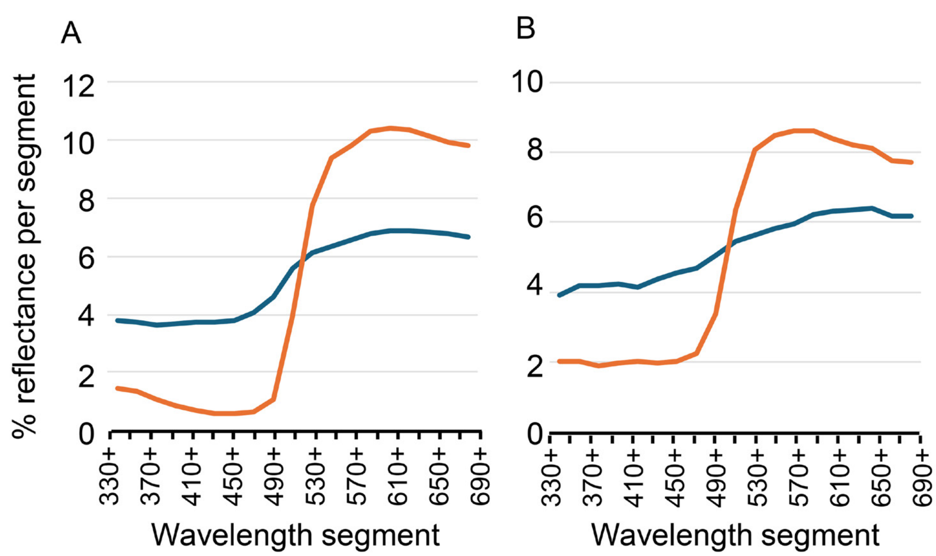

Figure 3. Examples of individual spectrometry graph plots of mean reflectance per wavelength segment - UV/grey versus orange/yellow dewlaps (the former in blue the latter in orange). **(A)** Both dewlap morphs found in *D. roquet* from each locality of transect A. **(B)** Dewlaps of *D. trinitatis* from Atlantic littoral habitat showing the UV/grey morph (localities 4 and 8 in Fig. 1a) and the montane habitat showing the typical orange/yellow morph (localities 1, 3, 7, 10 in Fig. 1a).

Table 1. Comparing UV/grey morph with other dewlaps. Comparing the UV/grey dewlaps of *D. trinitatis* from the Atlantic littoral habitat with the yellow/orange dewlaps from the other habitats using contrast ANOVA to compare two sets of localities indicates they are significantly different across all segments. Similarly, the two dewlap morphs present in *D. roquet* from in transect A in Martinique (Fig.1b) can be defined by the histogram in Fig. 2. These two morphs (pooled per morph irrespective of locality) are compared using t tests and these show that the reflectance is significantly different across the wavelength segment of the two dewlap morphs in for each of the 19 wavelength segments.

		D. trinitatis (df 34)				*D. roquet* (df 77) Transect A morphs			
Wavelength Segment (nm)	Seg #	% Area non-Atlantic littoral	% Area Atlantic littoral	t	P	% Area orange/ yellow morph	% Area UV/grey morph	t	P
330+	1	2.29	3.71	9.63	<.001	1.88	3.89	14.97	<.001
350+	2	2.13	3.54	10.24	<.001	1.86	4.17	16.48	<.001
370+	3	1.75	3.31	12.37	<.001	1.74	4.16	17.99	<.001
390+	4	1.43	3.34	15.56	<.001	1.81	4.21	18.22	<.001
410+	5	1.21	3.25	17.26	<.001	1.91	4.12	18.43	<.001
430+	6	1.08	3.11	17.19	<.001	1.96	4.34	19.90	<.001
450+	7	1.03	3.10	16.78	<.001	2.04	4.51	18.88	<.001
470+	8	1.13	3.38	17.72	<.001	2.27	4.66	15.05	<.001
490+	9	1.71	4.10	18.37	<.001	3.38	5.04	7.62	<.001
510+	10	4.48	5.57	6.90	<.001	6.20	5.48	4.52	<.001
530+	11	7.23	6.41	6.07	<.001	7.75	5.67	18.75	<.001
550+	12	8.44	6.81	11.40	<.001	8.21	5.83	17.46	<.001
570+	13	8.90	6.99	12.59	<.001	8.44	5.98	15.54	<.001
590+	14	9.36	7.30	13.78	<.001	8.61	6.27	17.00	<.001
610+	15	9.56	7.41	14.59	<.001	8.54	6.34	15.70	<.001
630+	16	9.60	7.37	14.80	<.001	8.48	6.39	13.58	<.001
650+	17	9.57	7.26	14.61	<.001	8.51	6.45	11.78	<.001
670+	18	9.58	7.13	14.21	<.001	8.18	6.22	10.30	<.001
690+	19	9.55	6.91	13.73	<.001	8.21	6.20	9.57	<.001

Atlantic littoral habitat compared to other habitats: St Vincent—*D. trinitatis*. The dewlap hue in individuals from the evergreen littoral Atlantic habitat has a rather flat spectrometry trace indicating a UV/grey hue to the dewlap (Fig. 3b). When the mean reflectance is compared between the habitat types, i.e. Atlantic littoral versus others (montane plus xeric) for each wavelength segment the Atlantic littoral means have significantly higher reflectance from the 330+ segment to the 510+ segment, while the other habitat means are significantly higher from the 530+ to 690+segments (Table 1, Fig. 3b, Fig. 5).

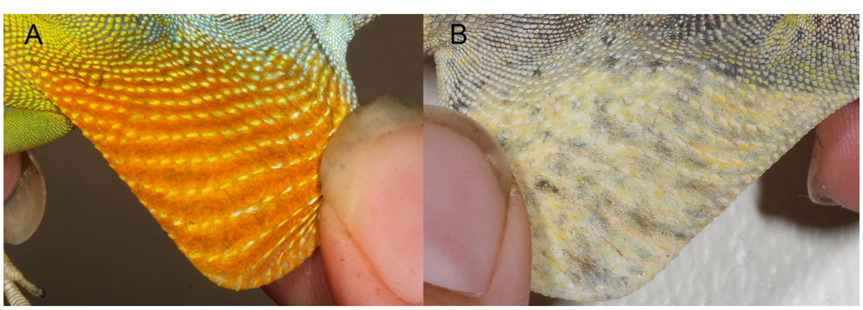

Figure 4. Photographic images of both dewlap morphs from *D. roquet* from transect A. **(A)** The more typical dewlap in the yellow to orange range. **(B)** The duller UV/grey dewlap. The respective spectrometry traces are in Fig. 3a.

Xeric versus montane habitats: Martinique—*D. roquet*. While the mean spectrometry traces for the xeric and montane habitats are broadly similar (Fig. 6a), both showing yellow/orange dewlaps (Fig. 7), the trace for the montane habitat rises more steeply showing a slightly more focal, saturated yellow/orange dewlap compared to those from the xeric habitat. Hence the montane means are significantly higher where it rises steeply at 530–629 nm, and subsequently lower at higher wavelengths 690–710 nm (Table 2).

Table 2. The dewlap hue from xeric and montane habitats in both *D. roquet* and *D. trinitatis* are compared using contrast ANOVAs. For both species, the dewlaps from montane habitats are significantly higher where the reflectance increases steeply (coded green) and subsequently significantly lower at the higher wavelengths (coded red). See text for explanation.

		D. trinitatis (df 34)				*D. roquet* (df 88)			
Wavelength Segment (nm)	Seg #	% Area Xeric	% Area montane	t	P	% Area Xeric	% Area montane	t	P
330+	1	1.65	2.03	3.03	0.005	2.32	2.22	0.87	>0.05
350+	2	1.58	2.04	3.47	0.001	2.24	2.12	1.02	>0.05
370+	3	1.48	1.91	3.34	0.002	1.84	1.60	2.56	0.012
390+	4	1.56	1.99	3.34	0.002	1.52	1.14	4.57	<0.001
410+	5	1.74	2.03	2.47	0.019	1.38	0.95	5.45	<0.001
430+	6	1.92	1.98	0.43	>0.05	1.33	0.87	5.48	<0.001
450+	7	2.04	2.04	0.10	>0.05	1.32	0.84	5.52	<0.001
470+	8	2.32	2.24	0.53	>0.05	1.46	0.96	4.89	<0.001
490+	9	3.37	3.38	0.02	>0.05	2.07	1.60	3.12	0.002
510+	10	5.92	6.38	3.09	0.004	4.64	4.64	0.04	>0.05
530+	11	**7.29**	**8.06**	**7.07**	**<0.001**	**7.17**	**7.95**	**6.17**	**<0.001**
550+	12	**7.82**	**8.48**	**4.87**	**<0.001**	**8.40**	**9.35**	**9.40**	**<0.001**
570+	13	8.19	8.61	2.73	0.05	**8.91**	**9.86**	**9.16**	**<0.001**
590+	14	8.61	8.61	0.027	>0.05	**9.25**	**10.12**	**7.90**	**<0.001**
610+	15	8.76	8.39	2.63	0.013	**9.41**	**10.01**	**4.90**	**<0.001**
630+	16	**8.88**	**8.21**	**4.34**	**<0.001**	9.38	9.66	1.91	>0.05
650+	17	**9.06**	**8.14**	**5.27**	**<0.001**	9.25	9.13	0.70	>0.05
670+	18	**8.83**	**7.74**	**5.66**	**<0.001**	9.12	8.70	2.19	0.031
690+	19	**8.96**	**7.72**	**5.88**	**<0.001**	**8.98**	**8.27**	**3.38**	**0.001**

Xeric versus montane habitats: St Vincent—*D. trinitatis*. As with *D. roquet*, while the mean spectrometry traces for the xeric and montane habitats are broadly similar (Fig. 6b), both showing yellow/orange dewlaps (Fig. 5), the trace for the montane habitat rises more steeply showing a slightly more focal, saturated yellow/orange dewlap compared to those from the xeric habitat. Hence, the montane means are significantly higher from where it rises steeply at 530–569 nm, and subsequently lower at the higher wavelengths at 630–710 nm (Table 2).

Dewlap hue and the allopatric model speciation. Transect A, shows a sharp change in lineage associated with the precursor islands and this is associated with a degree of genetic isolation between these two previously allopatric lineages commensurate with model of allopatric speciation. The percentage frequency of the yellow/orange dewlap morph (versus UV/grey dewlap) is 78, 50, 20, 40, 10, 70, 40, 20 from north to south along transect A, and hence does not appear to be related to the precursor island lineage and genetic structure associated with allopatric divergence (Fig. 8a).

Dewlap hue and ecological model of speciation. Transect B shows a change in habitat between xeric and montane rainforest (within the same precursor island lineage) and is associated with a genetic structure commensurate with a model of ecological speciation with the ecotone between sites B3 and B4. Here, the change in dewlap hue is associated with the genetic structure and ecotone (Fig. 8b). A contrast ANOVA comparing dewlap hue (expressed as CV1) either side of the ecotone shows this is significant ($t = 8.55$, $df = 63$, $P < 0.001$).

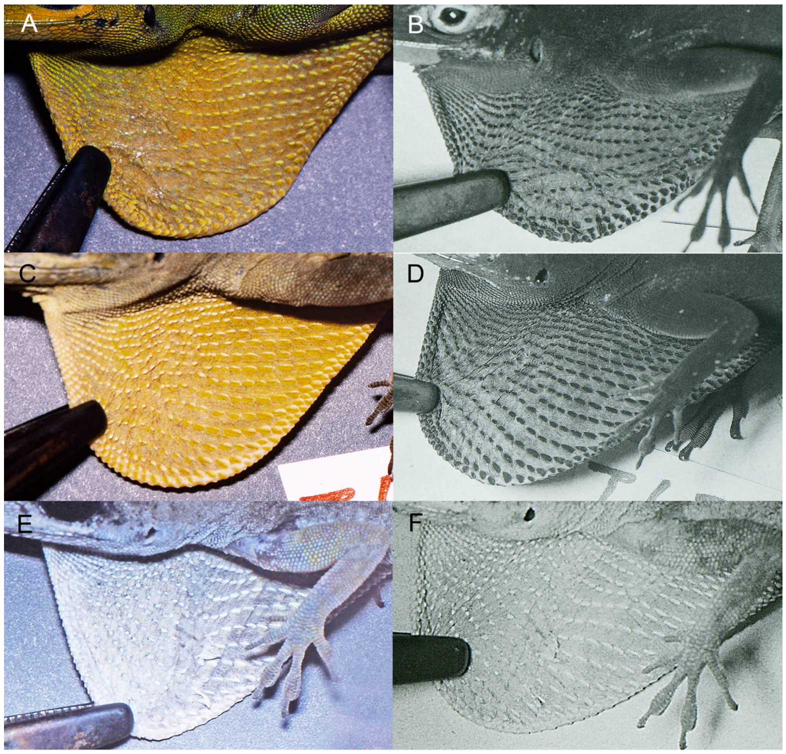

Figure 5. Photographic images of dewlaps of *D. trinitatis*, St. Vincent. Top row montane, middle row xeric and bottom row Atlantic littoral. Left column conventional RGB image, right column UV reflectance only. The montane **(A)** and xeric **(C)** habitat dewlaps are yellow/orange (left column) without UV reflectance (**B, D** respectively), while the dewlap from the Atlantic littoral habitat appears light greyish **(E)** with strong UV reflectance **(F)**.

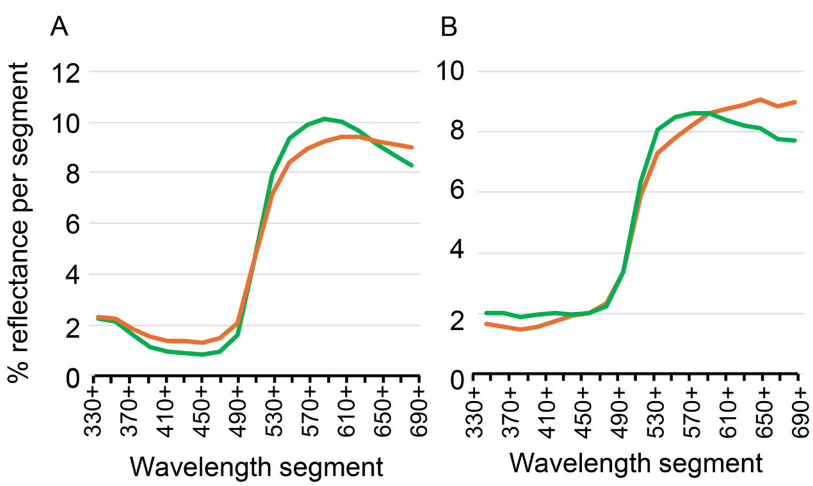

Figure 6. Spectrometry graph plots of mean reflectance per wavelength segment for dewlaps from xeric versus montane habitats. **(A)** *D. roquet,* Martinique. **(B)** *D. trinitatis,* St. Vincent. In both species the mean dewlap hue is broadly similar in both montane (green line) and xeric (orange line) habitats, i.e. a yellow/orange hue dewlap. However, both graphs show that the trace for the dewlap from the montane habitat is more focal (i.e. intense or saturated in hue) as it rises more steeply and then drops at the higher wavelengths.

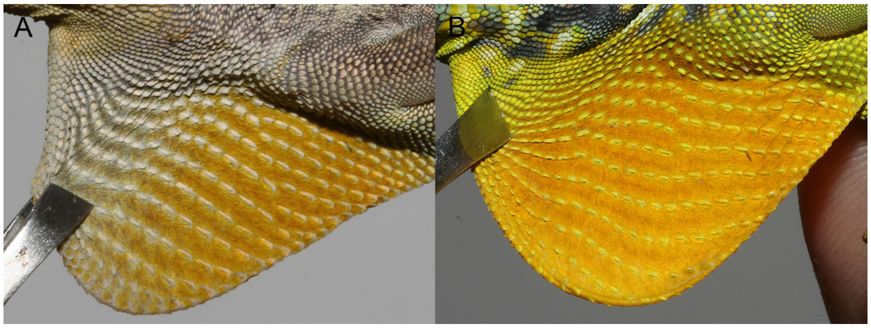

Figure 7. Photographic images of both dewlap morphs from *D. roquet*. **(A)** Xeric habitat. **(B)** Montane habitat. Localities B1 and B7, respectively in Fig. 1b.

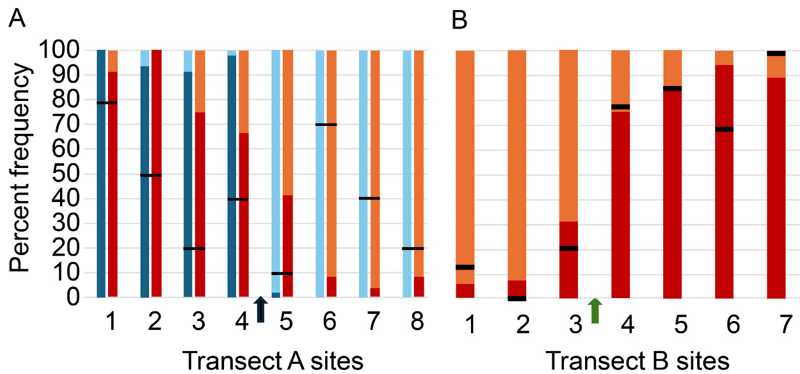

Figure 8. (A) Allopatric speciation paradigm. The frequency of the two mtDNA lineages (dark blue NW lineage, light blue central lineage) and genetic structure (two groups defined by hypervariable nDNA, orange and red) along transect A (Fig. 1b) both taken from Thorpe *et al.* (2010). The black bars show the frequency of the typical orange dewlap in relation to lineage and genetic structure. The division between the two precursor islands is between sites 4 and 5 and shown by a black arrow. **(B)** Ecological speciation paradigm (within the same precursor island lineage). The frequency of the two genetic structure groups along transect B (Fig. 1b), with the ecotone between the xeric sites (1-3) and montane sites (4-7) indicated by a green arrow. The black bars indicate the overall hue of the dewlap as summarized by canonical variate 1 run on the 19 wavelength segments as variables.

Discussion

Although geographic variation in dewlap hue within a species is not uncommon in anoles (Thorpe 2002; Thorpe *et al.* 2010; Losos 2009; Ng & Glor 2011; Ng *et al.* 2016; Glor & Laport 2012; Scherrer *et al.* 2022) distinct polymorphism within a local population across a region is uncommon and has not previously been recorded in Lesser Antillean anoles. Stapley *et al*. (2011) show that the Central American anole *Norops* (previously *Anolis*) *apletophallus* has either a solid orange dewlap, or with the orange limited to the centre and a white margin. This varies geographically with most population having a single morph, but just two sites from one area have both morphs showing within-population polymorphism. The Martinique anole, *D. roquet*, has widespread within-population polymorphism along the NE Atlantic coast with both the more standard yellow/orange hue and the more unusual UV/grey hue (this is solely a matter of hue and not pattern as in *N. apletophallus*). No population on Martinique was found with just the UV/grey morph and there are no reported cases of such within-population polymorphism in other Lesser Antillean anoles from either the northern or southern genera.

Crawford *et al.* (2023) have investigated the genetic basis of body coloration in an anole and Behere *et al.* (2024) have suggested dewlap polymorphism is a simple Mendelian trait in *Ctenonotus distichus*. While anoles have been the subject of gene discovery (Rodriguez *et al.* 2017) little is known of the specific genes controlling dewlap hue in anoles, or the genes involved in UV markings. This polymorphism in NE Martinique provides an opportunity to investigate candidate genes, as the polymorphism within a single locality avoids the complication of among-locality genetic variation.

Parallel evolution (Arendt & Reznick 2008; Wake *et al.* 2011), particularly variation among independent island populations in relation to parallel changes in habitat (Brown *et al.* 1991; Thorpe 2017; Thorpe *et al.* 2015), provide evidence for the role of natural selection. In both *D. roquet* from Martinique and *D. trinitatis* from St. Vincent, the populations from the Atlantic littoral habitat (Malhotra 2022) have the unusual UV/grey dewlap hue, albeit polymorphic in the former and fixed in the latter. The difference between the reflectance spectrographs of UV/grey and yellow/orange dewlaps is very pronounced in both species and is strongly significant at every wavelength segment. These results point to notable parallel evolution and imply adaptation to this habitat by natural selection. However, the details of this adaptation are unclear. Perhaps the nature of the low incidence light at sunrise through the evergreen littoral vegetation is a factor that favours a light UV/grey dewlap.

While the difference between UV/grey and the more general yellow/orange dewlaps is pronounced, the difference between xeric and montane dewlaps is subtle in both *D. roquet* from Martinique and *D. trinitatis* from St. Vincent. Nevertheless, a comparison between xeric and montane dewlaps within a species is very similar for both species, and both species have significantly different reflectance between these habitats at key wavelength segments (Table 2). The montane dewlap has a more saturated, focal colour, compared to the xeric dewlap. This is compatible with Ng *et al.*'s (2013) finding that "dewlaps tend to be more orange in cooler environments with more tree cover" but not with Fleishmann *et al.*'s (2022) finding that "white" dewlaps are more common in Greater Antillean ecomorphs from darker habitats or the general expectation that desaturated hues reflect more photons than saturated hues and this would benefit being seen in the lower light conditions of the rainforest. Whatever the basis for this parallel evolution it implies adaptation by natural selection to these two different habitats.

Although distinct within-island phylogeographic lineages are widespread within Lesser Antillean anoles (Thorpe *et al.* 2018), in the south, there is only one clear case where there appears to be sufficient restriction in gene flow between them to imply the process of at least partial allopatric speciation. This occurs in *D. roquet* in the coastal area of NE Martinique where the NW and central precursor island meet after a considerable time as separate entities (Thorpe *et al.* 2010). The anole population on these precursors would have met secondarily after being able to diverge in geographic isolation compatible with the allopatric model of speciation. These two lineages look very phenotypically distinct in this region (Fig. 9 a, b) and the transition across the contact zone is marked and over a short geographic distance (Johansson *et al*. 2008, Thorpe *et al.* 2010). These are not recognised as distinct species because this categorical difference in phenotype and genetic structure is not maintained along the length of the contact zone when it extends into the montane habitat. However, if the dewlap hue is critically important as a pre-mating isolating mechanism, then one would expect the frequency of the dewlap morphs (UV/grey versus yellow/orange) to relate to the change in lineage and the genetic structure reflecting the reduced gene flow between lineages at the coast. However, there is no such relationship (Fig. 8a). Moreover, the climate changes gradually along this transect (Thorpe *et al.* 2010) and the morph frequency, being haphazard, does not relate to this either. The sample size used in spectrometry (~10 per locality) is less than Thorpe *et al*. (2010) used for lineage and genetic structure frequency (~48 per locality), and it may be insufficient for a reliable estimate of frequency change along this transect. Further insight into the relationship between adaptation to abiotic and biotic factors and/or the role of dewlap hue as a pre-mating isolating mechanism may be gained by 1) a much larger sample per locality to give a reliable estimate of dewlap morph frequency, and 2) a more comprehensive selection of localities across the contact zone and habitat types.

On the west facing elevation on northern Martinique, within the NW lineage, there is a distinct change in habitat from a more coastal xeric habitat to montane rainforest at higher elevations (Thorpe *et al.* 2010). Here, the level of genetic isolation between habitat types is even greater than between precursor island lineages in transect A (Thorpe *et al.* 2010) and is compatible with the model of ecological speciation (Nosil 2012). In contrast, to the allopatric model in transect A, here the change in dewlap hue along the xeric-montane transect is compatible with the genetic structure predicted by the ecological speciation. This is in line with the parallel evolution of xeric-montane dewlap hue discussed above and is compatible with the sensory drive (Endler 1992) concept of signals being adapted to the environment driving isolation. Although xeric and montane dewlaps are significantly different, some caution is appropriate because the difference between dewlap hues is subtle and far less than the pronounced difference in body hue and pattern between xeric and montane phenotypes (Fig. 9, c, d). Moreover, behavioural factors independent of hue (e.g., head-bobbing), may also play a role in recognition. Hence, although dewlap hue may play a role in reproductive isolation, there is not robust evidence for it in these examples (Ng *et al.* 2017, Scherrer *et al.* 2022) and a clearer resolution of this question may lie in direct experimentation.

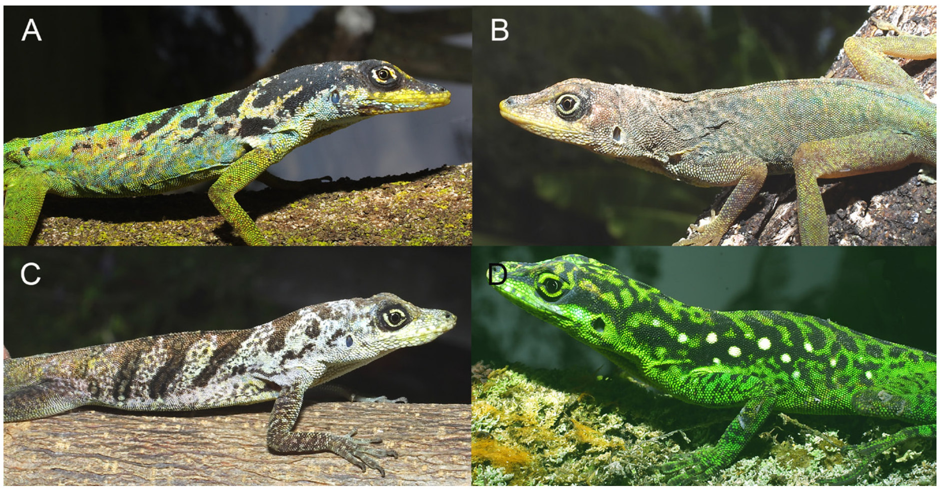

Figure 9. *Dactyloa roquet* adult males. **(A)** Transect A, NW lineage. **(B)** Transect A, central lineage. **(C)** Transect B, xeric. **(D)** Transect, B montane.

Acknowledgments

We thank Anita Malhotra and two anonymous reviewers for their comments on earlier drafts of the manuscript.

References

Arendt J, Reznick D. 2008. Convergence and parallelism reconsidered: what have we learned about the genetics of adaptation? *Trends in Ecology and Evolution* 23: 26–32. **Article**

Behere A, de Mello P, Geneva J, Glor RE. 2024. The genetic architecture of dewlap pattern in Hispaniola anoles (*Anolis distichus)*. *Evolution*, 78: 987–994. **Article**

Brown RP, Thorpe RS, Báez M. 1991. Parallel within-island microevolution of lizards on neighbouring islands. *Nature* 352: 60–62. **Article**

Crawford NG, McGreevy TJ Jr., Mullen SP, Schneider CJ. 2023. The genetic basis of conspicuous coloration in the Guadeloupean anole: Evolution by sexual and ecological selection. *Ecology and Evolution* 13: e10266. **Article**

Endler JA. 1992. Signals, signal conditions, and the direction of evolution. *The American Naturalist*, 139: 125–153. **Article**

Fleishman LJ, Perez-Martinez CA, Leal M. 2022. Can sensory drive explain the evolution of visual signal diversity in terrestrial species? A test with Anolis lizards. *The American Naturalist* 200: 236–249. **Article**

Glor RE, Laport RG. 2012. Are subspecies of *Anolis* lizards that differ in dewlap color and pattern also genetically distinct? A mitochondrial analysis. *Molecular Phylogenetics and Evolution* 64: 255–260. **Article**

Johansson H, Surget-Groba Y, Thorpe RS. 2008. The roles of allopatric divergence and natural selection in quantitative trait variation across a secondary contact zone in the lizard Anolis roquet. *Molecular Ecology* 17:

5146–156. **Article**

Leal, M., and L. J. Fleishman. 2004. Differences in visual signal design and detectability between allopatric populations of Anolis lizards. *American Naturalist* 63: 26–39. **Article**

Losos JB. 2009. Lizards in an evolutionary tree. University of California Press. 507 p.

Malhotra A. 2022. Vegetation. In: Thorpe, Reptiles of the Lesser Antilles. Edition Chimaira, Frankfurt. 608 p.

Maury RC, Westbrook GK, Baker PE, Bouysse P, Westercamp D. 1990. Geology of the Lesser Antilles. In: Dengo G, Case JE, editors. The geology of North America: Geological Society of America (Boulder, CO), p. 141–166.

Ng J, Geneva AJ, Noll S, Glor RE. 2017. Signals and speciation: *Anolis* dewlap color as a reproductive barrier. *Journal of Herpetology* 51: 437– 447. **Article**

Ng J, Glor RE. 2011. Genetic differentiation among populations of a Hispaniolan trunk anole that exhibit geographical variation in dewlap colour. *Molecular Ecology* 20: 4302–4317. **Article**

Ng J, Landeen EL, Logsdon RM, Glor RE. 2013. Correlation between Anolis lizard dewlap phenotype and environmental variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution* 67: 573–582. **Article**

Ng J, Ossip-Klein AG, Glor RE. 2016. Adaptive signal coloration maintained in the face of gene flow in a Hispaniolan Anolis Lizard. *BMC Evolutionary Biology* 16: 193. **Article**

Nosil P. 2012. Ecological speciation. Oxford, UK: Oxford University Press. 304 p.

Ogden R, Thorpe RS. 2002. Molecular evidence for ecological speciation in tropical habitats. *Proceedings of the National Academy of Sciences of the United States of America* 99: 13612–13615. **Article**

Rodríguez A, Rusciano T, Hamilton R, Holmes L, Jordan D, Wollenberg Valero KC. 2017. Genomic and phenotypic signatures of climate adaptation in an *Anolis* lizard. *Ecology and Evolution* 7: 6390–6403. **Article**

Scherrer R, Donihue CM, Reynolds RG, Losos JB, Geneva AJ. 2022. Dewlap colour variation in Anolis *sagrei* is maintained among habitats within islands of the West Indies. *Journal of Evolutionary Biology* 35: 680–692. **Article**

Stapley J, Wordley C, Slate J. 2011. No evidence of genetic differentiation between anoles with different dewlap color patterns. *Journal of Heredity*, 102: 118–124. **Article**

Surget-Groba, Y., H. Johansson & R. S. Thorpe. 2012. Synergy between Allopatry and Ecology in Population Differentiation and Speciation. *International Journal of Ecology* 2012: 273413, 10 pages. **Article**

Surget-Groba Y, Thorpe RS. 2013. A likelihood framework analysis of an island radiation: phylogeography of the Lesser Antillean gecko *Sphaerodactylus vincenti*, in comparison with the anole *Anolis roquet*. *Journal of Biogeography* 40: 105–116. **Article**

Thorpe RS. 2002. Analysis of color spectra in comparative evolutionary studies: molecular phylogeny and habitat adaptation in the St. Vincent anole (*Anolis trinitatis*). *Systematic Biology* 51: 554–569. **Article**

Thorpe RS. 2017. Predictability in evolution: Adaptation of the Bonaire anole (*Anolis bonairensis*) to an extreme environment. *Public Library of Science ONE* 12(5): e0176434. **Article**

Thorpe RS. 2022. Reptiles of the Lesser Antilles. Edition Chimaira, Frankfurt. 608 p.

Thorpe RS, Barlow A, Malhotra A, Surget-GrobaY. 2015. Widespread parallel population adaptation to climate variation across a radiation: implications for adaptation to climate change. *Molecular Ecology* 24: 1019–1030. **Article**

Thorpe RS, Barlow A, Surget-Groba, Y. Malhotra A. 2018. Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles. *Molecular Phylogeny and Evolution* 127: 682–695. **Article**

Thorpe RS, Reardon JT, Malhotra A. 2005. Common garden and natural selection experiments support ecotypic differentiation in the Dominican anole (*Anolis oculatus*). American Naturalist 165: 495–504. **Article**

Thorpe RS, Richard M. 2001. Evidence that ultraviolet markings are associated with patterns of molecular gene flow. *Proceedings of the National Academy of Sciences* 98: 3929–3934. **Article**

Thorpe RS, Stenson AG. 2003. Phylogeny, paraphyly and ecological adaptation of the colour and pattern in the

Anolis roquet complex on Martinique. *Molecular Ecology* 12: 117–132. **Article**

Thorpe RS, Surget-Groba Y, Johansson H. 2008. The relative importance of ecology and geographic isolation for speciation in anoles. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 3071–3081. **Article**

Thorpe RS, Surget-Groba Y, Johansson H. 2010. Genetic tests for ecological and allopatric speciation in anoles on an island archipelago. *Public Library of Science Genetics* 6: e1000929. **Article**

Wake DB, Wake MH, Specht CD. 2011. Homoplasy: from detecting pattern to determining process and mechanism of evolution. *Science* 331: 1032–1035. **Article**