

**UNIVERSIDAD DE LOS ANDES**  
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**How do opposing pressures of sexual and natural selection in  
continental and insular settings shape the evolution of coloration in a  
tropical gecko?**

**Mateo Dávila-Játiva**

**Director**

**Carlos Daniel Cadena PhD**

**Co-Director**

**Diego Cisneros-Heredia PhD**

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Mateo Dávila-Jativa<sup>1, 2, 3, 4</sup> Lía Altamirano<sup>2, 3, 5</sup>, Diego Cisneros-Heredia<sup>2, 3, 4</sup>, Maria De Lourdes Torres<sup>3, 4, 5</sup> and Carlos Daniel Cadena<sup>1</sup>

1. Departamento de Ciencias Biológicas, Laboratorio de Biología Evolutiva de Vertebrados, Universidad de los Andes, Bogotá, Colombia
2. Universidad San Francisco de Quito USFQ, Instituto de Diversidad Biológica Tropical iBIOTROP, Museo de Zoología & Laboratorio de Zoología Terrestre, Quito 170901, Ecuador
3. Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas y Ambientales COCIBA, Quito, Ecuador
4. Galápagos Science Center, Universidad San Francisco de Quito USFQ & University of North Carolina at Chapel Hill UNC
5. Universidad San Francisco de Quito (USFQ), Colegio de Ciencias Biológicas y Ambientales, Laboratorio de Biotecnología Vegetal, Campus Cumbayá, Quito, Ecuador

## 1. Introduction.

Natural selection favors traits that are advantageous for the survival of individuals in a given environment [1,2], whereas sexual selection favors traits which may enhance reproduction despite being costly to produce and frequently detrimental to the survival of the bearer of the trait [3,4]. In animal coloration, for example, more conspicuous and ornamented patterns might be favored by sexual selection, but such patterns may also increase predation risk [5–10]. Opposing pressures of sexual and natural selection may thus result in tradeoffs, having a profound effect on the evolution of coloration in animals.

In several animals, predation pressure correlates with conspicuousness in coloration, such that species that evolved in areas with more predators, or inhabit more open areas where they might be more exposed to predation, tend to be more cryptic than their counterparts evolving relatively free of predation [11–15]. Opposing pressures of natural and sexual selection influencing coloration have been experimentally demonstrated in guppies (*Poecilia reticulata*), in which increases in predation pressure on populations formerly unexposed to predators caused them to become more cryptic within a few generations, whereas reducing predation pressure on populations caused individuals to become more colorful and ornamented [16,17].

Appropriate systems in which one may assess the role of tradeoffs in traits under sexual and natural selection driving the evolution of phenotypes are those in which populations occur in distinct environments differing in predation pressure, such as continents and islands [18–20]. In particular, the evolution of sexually selected animal species on islands in relation to predation pressure may proceed along two alternative paths. On one hand, animals on islands are expected to experience lower predation pressure due to depauperate predator assemblages [21–25], resulting in predation release leading to evolutionary changes in island populations to produce

patterns including insular gigantism [26,27], reduction in dispersal abilities [28,29], and reduced fecundity and slower developmental periods [30,31]. Regarding coloration, sexual selection for conspicuouness may overcome natural selection for crypsis in some insular populations, where individuals are less cryptic than their continental counterparts [32]. On the other hand, island species may evolve to become less colorful and duller than their continental counterparts possibly due to relaxation of several pressures related to sexual selection and species recognition [18,33]. Additional work is necessary to determine the generality of such patterns, particularly regarding the evolution of color in islands in reptiles, which have been little studied [32,34].

*Gonatodes caudiscutatus* is a terrestrial, mostly diurnal gecko (Sphaerodactylidae) with strong sexual dichromatism. Males have bright yellow-orange throats, yellow-orange patterns on their heads and blue spots on their sides, whereas females exhibit an inconspicuous brown and black coloration [35,36]. *G. caudiscutatus* is broadly distributed west of the Andes from northern Ecuador to northern Peru. This gecko occupies a wide range of habitats differing in vegetation structure and types of terrestrial substrates, in which populations have presumably evolved under strong predation pressure because of their occurrence in tropical lowlands where predator assemblages are rich [37–39]. Additionally, a population of *G. caudiscutatus* was introduced to San Cristobal Island in the Galapagos Archipelago [40], with the first reports on the island dating back to 1891 under the incorrect assumption that it was a new endemic species then described as *Gonatodes collaris* [35,41,42]. San Cristobal is a relatively small island 930 km off the coast of Ecuador with an impoverished biodiversity typical of islands and very few potential predators, particularly for introduced species [22,25].

We explored how the natural and sexual selection tradeoff is resolved in environments varying in levels of predatory pressure and sexual selection, taking advantage of the natural experiment offered by the geographic distribution of *G. caudiscutatus* including a presumably predator-rich native range and a non-native insular range with likely reduced predator pressure. Specifically, we measured predation pressure in continental and insular populations and asked how conspicuousness (color contrast with their background) and colorfulness (color contrast between color patches and color volume) differ between continental and island geckos.

## 2. Methods

### 2.1 Study areas

This study took place over a substantial portion of the wide distributional range of *G. caudiscutatus*, covering three distinct ecosystems in continental Ecuador and two distinct climate areas in San Cristobal Island in the Galapagos Archipelago (Figure 1). In continental Ecuador, we sampled the following areas from north to south: (1) the northern humid lowlands to the west of the Ecuadorian Andes (hereafter referred to as Chocó) characterized by high humidity, with vegetation characteristic of humid tropical forests and frequent rain throughout the year [43,44]; (2) The western cordillera slopes (WCS), a tropical humid zone between 700 and 1300 m influenced by seasonality due to the rain shadow effect caused by the coastal and Andes cordillera [45]; and (3) the lowland dry forest (LDF) in southwestern Ecuador, characterized by arid and semi-arid climates with a strong seasonality linked to Humboldt's cold current [45]. Such habitat heterogeneity allowed us to assess whether continental geckos may have evolved to match their diverse environments as a result of predation, resulting in geographic variation in coloration. Because much of the Ecuadorian western lowlands and Andes slopes have been

deforested and turned into farming lands, towns or cities [46], several of our fieldwork locations were in urban or semirural areas.

San Cristóbal is an island located 930 km off of the continental coast and characterized by high annual seasonality, with a cold, dry season from July to November and a warm, wet season from December to June [47]. We conducted field work in the lowlands, which resemble the LDF in vegetation and climate, and in the highlands, characterized by cooler temperatures, richer soil, more abundant vegetation and more frequent rains in the rainy season [48] which resemble the continental WCS.

## 2.2 Field sampling

Between June 1 and September 3 2019, we conducted fieldwork in 52 locations in the western Andean slopes and western lowlands of continental Ecuador (37 sites) and in San Cristóbal Island in the Galapagos Archipelago (15 sites, Figure 1). At each location we exhaustively searched for geckos for  $\geq 3$  hours during the morning (between 8:00 and 11:00) or the afternoon (between 15:00 and 18:00) by moving rocks, logs, building material or any other movable object that could be used for hiding, and also by inspecting tree holes, crevices and spaces between reachable branches on bushes or trees. We sampled all locations in teams of two, so that when we spotted a gecko, one researcher would lift the covering object and the other would capture the gecko by hand. The geckos were then placed in plastic bags with a tag and a sample of the substrate (i.e. a handful) from the site where it was first spotted. We determined the age of geckos based on size and coloration, and obtained data only for adults. We collected coloration data on a total of 133 individuals: 68 in Galapagos (37 males, 31 females) and 65 in the continent (32 males, 33 females).

### 3. Quantifying predation pressure

Artificial animal models are often used to quantify predation pressure [9,10,49]. We experimentally measured predatory pressure in the field in continental and insular localities using models built with paraffin wax. We built 810 models using a silicone cast we made from a museum specimen of *G. caudiscutatus* using a two-part silicone solution [49]. We painted each paraffin model individually using non-toxic acrylic paint to resemble male color patterns based on available photographs (Figure 2A).

Each predation experiment consisted of placing 200-205 models along a 400 m transect in spots where we would typically expect to see *G. caudiscutatus*, next to potential hiding spots in areas with low bushes and in low tree branches. We always placed the models under the shade because we never spotted geckos exposed directly to the sun. The models were left in the field for 4 consecutive days with good weather conditions following published protocols [10]. After this time, models were collected and checked for bite, claw, or beak marks imprinted on the paraffin. Each marked model was photographed, the type of mark recorded along with information on where in the body was it attacked, and whether the attack had caused a limb, tail or head to break off.

A large number of marks were made by rodents and were usually spread around the model, as if animals nibbled on the paraffin or attempted to peel off the paint out of curiosity, potentially after being attracted to models by smell (Figure 2B). We did not consider these bites as predatory attacks, in keeping with work on introduced rats in Hawaii which do not prey upon adult vertebrates [50]. We also found that a large number of models disappeared, particularly in the island, where rodent populations are large [51,52]. Because several of the missing models were later found inside crevices or cavities near the spot where they had been originally placed and

always had rodent bite marks, we assumed that missing models were moved by rodents in the same proportion as models were attacked by rodents at each location. Accordingly, all rodent-related events were disregarded in our final attack counts.

We performed predation experiments in two island locations and two continental locations. Locations on the island were on the limit between the national park and the agricultural land in the highlands (NP) and in the Lab of Life grounds in the lowlands (LOL). Experiments in the continent were in Agua Blanca's community land in the province of Manabí (AB) and in the Cerro Blanco natural reserve in Guayas province (CB), both of them in the LDF region. The locations were chosen based on presence of *G. caudiscutatus* and on how remote they were from human populations, both to reduce the chances of people taking or tinkering with models and to reduce the disturbance effect of the presence of people on potential predator activity.

### 3.1 Reflectance measurements.

We quantified coloration of geckos and their environments using reflectance spectrophotometry. We took reflectance measurements using an Ocean optics USB4000 spectrophotometer fitted with an Ocean optics PX-2 pulsed xenon light source and a QR Premium Ocean Optics Reflection Probe.

We took measurements from six discernible color patches in males (yellow head patterns, dark head patterns, throat, dorsal line, blue side spots and dark sides) and from three discernible patches in females (head, dorsal line and dark sides; Figure 3). Each patch was measured three times (blue spots and dark sides where measured 3 times on each side) and later averaged per individual. We also took five measurements from random subsamples of the substrate samples

taken from the spot where each individual was first spotted to quantify background color and thus establish the conspicuousness of gecko coloration. We did this by emptying the content of the plastic bag where the substrate was transported onto a flat surface and flattening it into a square. We then took measurements from the top left, top right, bottom left, bottom right and center points of the substrate square; when the substrate was a single rock or a branch, we followed the same pattern on the shape the rock or log had.

We reflected light on the surfaces at a standardized  $90^\circ$  angle and at a 2 mm distance from the measured surface, which proved to result in the most stable curves on our specimens. We used an Ocean Optics WS-1-SL White Reflectance Standard and closed the tip of the probe to calibrate for white and dark standards, respectively, before measuring each specimen. We took all reflectance measurements within 8 hours of having captured the geckos and making sure individuals were within the temperature range at which they were usually found in the field, between 25 and 29 °C.

### 3.2 Reflectance data analysis

To work with reflectance spectra, we used R package *pavo* 2.0 [53]. First, we removed all negative reflectance values obtained due to electrical noise and performed a LOESS smoothing of all reflectance curves using the `prospec()` function. We then averaged all repeated measurements collected from each gecko and used the Tetrahedral Color Space Model [54] to calculate variables describing color variation and color contrast between individuals and their environment and between different color patches of individuals. This model incorporates information on sensitivity spectra of cones and luminance conditions to transform the reflectance spectra of color patches into points placed in a tetrahedral color space where each vertex represents the maximum

stimulation for each of the four cone types existing in the retina of birds [55]. To this end, we used the average ultraviolet-sensitive avian phenotype model built into *pavo* 2.0 given that all marks left on paraffin models resulted from bird attacks (see below). There is little or no information on the species of birds that feed on *G. caudiscutatus*, yet visual pigment characteristics are generally conserved across birds [56]. Therefore, we assumed that because an average of known bird visual models falls in the middle of the ranges of known peak sensitivity ranges for bird color pigments, it is likely a good approximation of those of any avian predator [57]. Because we never found a gecko exposed to direct sunlight but rather under canopy shade, we set environment illuminance for the model as forestshade in *pavo* 2.0.

To determine the conspicuosness of each gecko in its enviroment, we used the receptor noise model [58] as implemented in the `coldist()` function in *pavo* 2.0 to quantify chromatic contrast (dS) between the different color patches of each gecko and the 5 measurements of color of their corresponding substrate sample, and then averaged contrast values for each individual. Chromatic contrast is given in terms of just-noticeable-differences (JNDs). A JND value  $\geq 1$  between two patches of color indicatates these colors are distinguishable by the specified receptor given its visual system.

We also computed JNDs between adjacent color patches of male geckos (i.e. between blue spots and dark sides and between yellow and dark head patterns) as an indication of conspicuousness independent of the substrate. We also determined the color volume occupied by each male, defined as the minimum convex polygon cointaining all colors in a given individual [59], as a measure of color diversity [54].

We computed the color volume overlap (CVO) between color volumes from sets of 2 randomly selected males from the same sampling location in the Chocó, the Western Cordillera Slopes (WCS), and the Lowland dry forest (LDF) bioregions within and between populations. We also computed the CVO for all colors present on continental males and all colors present in insular ones and used this as a measure of overall color similarity [60] employing the `voloverlap()` function in *pavo*. We report the color volume dimension for each male or population and the v-smallest metric, defined as the volume of the overlap between two sets of color points divided by the volume of the smallest set of color points [54,59,61]. If one color volume is fully contained by the other, one expects a CVO value of 100%.

### 3.3 Statistical analyses

To compare predation pressure across locations where we conducted experiments, we first estimated the probability of being predated as the number of marked geckos over the total number of geckos placed at that location. We then computed the 90% confidence intervals for each location as if each model's probability of being attacked were constant and independent from that of other models. Under these assumptions, we can interpret each model as a Bernoulli experiment with a probability  $P$  of being attacked, whose standard error can be estimated with equation (1) and its 90% confidence intervals with equation (2):

$$(1) SE = \sqrt{p*(1-p)/n}$$

$$(2) IC = p \pm SE * Z(\alpha/2)$$

We considered a location's predation probability to be statistically different from others when their 90% confidence intervals did not overlap.

Kolmogorov-Smirnov[62] tests as implemented on the `ks.test()` function in R indicated that all our color contrast and color volume datasets departed from normality. We thus performed a Boxcox test [63], which showed that the best normalization method for all variables was a logarithmic transformation. After the transformation we tested for normality again and found that datasets approached normality but still departed from it. We nonetheless decided to use analysis of variance ANOVA tests on the transformed datasets given that this test is robust under moderate departures from normality [64]. To analyze color contrast data of each individual's color patch and their environment, we performed analyses of variance (ANOVA) for each color patch independently, with insularity (insular or continental) as the dependent variable, using the `lm()` function as implemented in R core's Stats package. We used the same procedure to analyze color contrast of adjacent patches data and of color volume data.

To take into account spatial effects (i.e. individuals are not equally independent from each other because of the geographic location where they were sampled), we fitted a linear mixed model (estimated using REML and `nloptwrap` optimizer) in which insularity was a fixed variable and type of ecosystem and collection location as random effects to predict color contrast for each color patch and their environment and for each pair of adjacent colors. In the case of color contrasts involving the blue spots (i.e. blue spots vs substrate, and blue spots vs dark sides) we used insularity as a fixed variable and collection location as random effects.

## 4. Results

### 4.1 Predation experiments.

Besides rodent marks, we exclusively found avian beak marks on our models, usually a single beak mark either on the head or on the tail (Figure 2C). Attacks by birds were visually confirmed

in one of the Galapagos locations, where, while placing the models, we spotted a San Cristobal Mockingbird (*Mimus melanotis*) attempting to prey upon one of them.

Disregarding rodent-related attacks for reasons described above, experiments suggested that predation pressure is greater in continental than in insular locations. We found a greater frequency of bird attacks on continental (7.4% in AB and 10.4% in CB) experiments than in insular ones (5.0% in NP and 4.3% in LOL). Predation probability was significantly higher in the CB continental location than in both insular locations; the confidence intervals for predation probability between the AB continental location and the insular locations overlapped, but there was a clear trend for higher probabilities of predation in this continental site as well.

#### 4.2 Color variation

We found substantial variation in male coloration both between and within populations throughout the range of *G. caudiscutatus*. Males in each population ranged from having very dark background colors and very bright color patches to lighter backgrounds and duller patches, showing color volume overlap values within a population of as low as 22% (in the Chocó) and of 45% on average. Variation was considerably higher among populations, with values of color volume overlap between sites being as low as 0.015% (a gecko from the cordillera vs. one from the southern dry forest) and of 21% on average (Figure 1). Male geckos throughout their distribution seemingly occupied similar color volumes, but overlap in space was often reduced. Regardless of the variation throughout its continental distribution and the metric used, continental geckos appeared to be more conspicuous than insular ones, and several metrics suggested that insular populations are more variable than continental ones as described below.

Darker base colors (dark head color patterns, dark sides and dorsal lines) showed little variation between continental and insular individuals, but the brighter patches only present in males (blue spots, yellow head patterns and throat) were consistently more contrasting relative to the background substrate in continental than in insular males. Geckos in continental populations exhibited significantly more conspicuous yellow head color patterns and throats than insular ones, with average contrast to the background measurements well above the 1 JND discriminability threshold given avian vision, whereas the mean for insular males was below this threshold. The blue spot color contrast was, on average, well above the threshold both for continental and insular males, yet continental males were significantly more contrasting than insular ones when compared to their dark sides. Additionally, insular geckos showed greater variance in the blue spot color contrast than continental ones (Figure 5 A).

The same pattern was observed when comparing adjacent colors within each male gecko (yellow head color patterns to dark head color patterns and blue spots to dark sides): continental males were significantly more contrasting on head color patterns, with no measurements below the 1 JND threshold. In turn, insular geckos showed a lower mean contrast and some measurements were below the discrimination threshold. Likewise, continental geckos showed a higher mean contrast between the blue spot and the dark sides than insular geckos, in which some measurements were below the discrimination threshold and variance was greater (Figure 5 B).

In terms of color volumes, continental males were significantly more colorful than insular ones (Figure 5 C). Color volume overlap between all insular and all continental colors together was 87% and insular volume (0.00054) was larger than the continental one (0.00049). This reveals that although individual continental males are more colorful than insular ones, there is a larger

variety of colors present in the island than in continental locations despite the much wider geographic scatter of the latter in mainland Ecuador.

## 5. Discussion

Our study experimentally demonstrated that populations of the gecko *G. caudiscutatus* likely experience lower predation pressure in San Cristobal Island in the Galapagos than in localities in mainland Ecuador as expected given depauperate predator assemblages in insular settings [25,65]. However, our inference of reduced predation pressure in the island was not associated with greater conspicuousness in male coloration as predicted by the hypothesis that tradeoffs between the outcomes of sexual selection and natural selection should be resolved in favor of the former where predation pressure is lower [9,17,32,57]. In contrast, we found evidence consistent with previous work indicating that some insular animals have less elaborate signals than their continental counterparts. Several hypotheses have been proposed to explain evolution towards less conspicuous animals in islands including mechanisms related to life-history tradeoffs, reduced intersexual selection, and reduced interspecific interactions. We discuss these hypotheses below in the context of our study system, noting that ours is one of the first studies on the evolution of coloration of dichromatic reptiles in insular settings.

Because island birds invest more in parental care and offspring quality than their mainland counterparts [31], it has been proposed that insular animals may become less colorful as a result of differential trade-offs between investment in parental care and sexual secondary traits in islands vs. continents [18]. This hypothesis would appear unlikely to apply to our study system because *G. caudiscutatus* has no reported parental care mechanism other than communal egg laying [66], and no differences have been documented in parental investment between islands and

continents. However, assessing trade-offs acting on other life-history characteristics which may differ between island and continental populations would be necessary to further examine this hypothesis. For example, it is possible that self-maintenance and longevity may be favored over traits influencing mate attraction in insular populations [67], but this has not been studied in *G. caudiscutatus*.

A second hypothesis is that reduced animal conspicuousness in islands is the consequence of reduced intersexual selection, a pattern which may arise through various mechanisms [18]. First, because lower genetic diversity within island populations is expected as a result of founder effects, bottlenecks and lower population size [68,69], the genetic makeup of different males is expected to be quite similar on islands. If this were the case, then indirect benefits of mate choice, such as passing “good genes” onto offspring, are predicted to be lower on islands than in continental populations with greater genetic variation among males [70]. However, it is also possible that intersexual selective pressures are not affected by island life, but rather that the genetic makeup of the island populations, influenced by the variation involved in island colonization events, may be such that brighter males simply cannot be produced.

A reduction in sexual selection in islands may also be due to impoverished parasite assemblages, given the hypothesis that complex and conspicuous secondary sexual characteristics may evolve as signals of parasite resistance [71], although evidence linking parasite pressure and coloration is mixed in birds [72–74] and lizards [75,76]. Because some groups of parasites in the Galapagos Archipelago are indeed depauperate [77], a release from parasite pressure in insular populations could result in relaxed sexual selection explaining, at least in part, the lower conspicuousness and greater color variation we reported in this study. To test this hypothesis, one could survey

parasites affecting *G. caudiscutatus* throughout its native and introduced distribution, and relate parasite pressure (i.e. parasite diversity and abundance) with color conspicuousness and measures of sexual selection.

Another mechanism resulting in less intense sexual selection in islands is that increased longevity on islands [78,79] could be associated with lower divorce rates and longer pair bonds, which should result in lower variance among individuals in lifetime breeding success [80]. There is no specific information available on the mating system of *G. caudiscutatus* or in other member of the genus, yet the most common system for other dichromatic geckos in the genus *Sphaerodactylus* is promiscuous mating [81]. Therefore, hypotheses related to long-term pair bonding would seemingly not apply to our study species, but information on its social and mating system would be needed to confirm this.

Finally, a reduced pressure for interspecific recognition associated with low species richness on islands may result in reductions in signal complexity. Accordingly, continental bird species living in sympatry with more same-family species than their insular counterparts exhibit more elaborate visual signals, probably as a result of selection against hybridization [18]. Our data support this idea to the extent that males from the continent are more conspicuous than their insular counterparts, and populations of *G. caudiscutatus* are sympatric with several other members of the Sphaerodactylidae family throughout its continental distribution and not in the island. This idea could be further assessed by comparing metrics of the conspicuousness of continental *G. caudiscutatus* relative to overlap with other gecko species. However, substantial effort is still needed to fully understand the distributions of small reptiles in continental Ecuador so that such tests could be properly performed.

The differences we observed between insular and continental geckos in color contrast were quite clear in comparisons involving yellow head patterns or throat coloration, but were less obvious in comparisons involving the blue spots on the sides of males. This could be the outcome of different color patches being affected by different selective pressures [12,82], as colors that are hidden to predators but visible to conspecifics are likely under different selective pressures than those exposed to all. This may explain our findings for throat color in *G. caudiscutatus*, but how would it apply to yellow head patterns is perhaps less obvious. We speculate that head color patterns might work as disruptive coloration [83,84] allowing animals to blend with their background [85] when seen from above by potential predators, while serving as signals to conspecifics when seen from the side (Figure 6). Further studies that include spectral data but also consider how these colors are distributed on individuals, as well as experimental tests of the function of different color patches in alternative contexts, would be an exciting next step towards understanding conspicuousness from the point of view of predators and conspecifics.

Species in which populations have been introduced to islands represent unique natural experiments allowing one to assess effects of different selective forces driving the evolution of phenotypic traits [32,34,86]. However, introduced populations also imply difficulties at different levels. *G. caudiscutatus* is believed to have arrived to the Galapagos Archipelago by means of cargo boats from the city of Guayaquil [41], with the first reports of its presence in the island dating back to the late 1800's [35]. The c. 130 years passed since the first reports of *G. caudiscutatus* in the island is arguably a short time frame for evolution to act on a vertebrate population, even under substantially different selection pressures. Additionally, nothing is known about how many times and from where exactly was the species introduced into San Cristobal.

Attempts to elucidate such colonization history by our group using phylogeographic analyses of mitochondrial and nuclear DNA sequences were inconclusive (M. Dávila-Jativa *et al.*, in prep) and even if we knew the continental origin of the insular population, it would be impossible to know the coloration of the founding geckos and this could have important effects on the current insular population's color. Additionally, we believe that multiple introductions are likely in the island, because most goods still arrive to the island by means of cargo boats. Although even if there is recurrent gene flow from the continent to the mainland genetic differences may arise between populations if selection is strong [87], we cannot rule out the possibility that the patterns we observed reflect phenotypic plasticity rather than genetic divergence and adaptation [86,88]. Integrating additional ecological, morphological and genetic analysis in future studies would allow painting a clearer picture on how tradeoffs in traits subject to natural and sexual selection are resolved to drive the evolution of coloration and conspicuousness in *G. caudiscutatus* and other species occurring in continental and insular settings.

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## Figures and tables

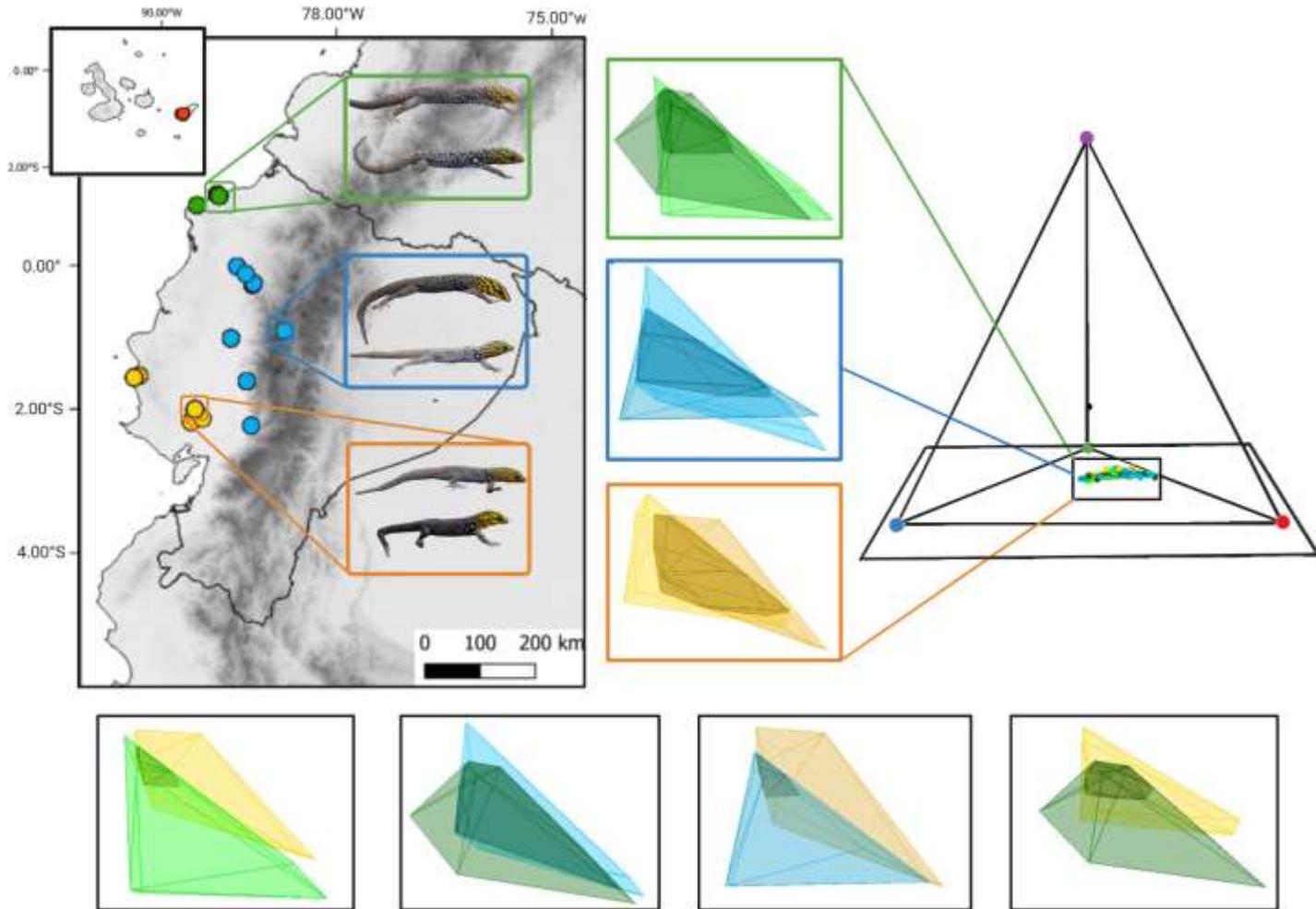


Figure 1. Map showing sampling locations in continental Ecuador and San Cristobal island along with photographs of male geckos captured in 3 different continental ecosystems showing examples of their color variation. For each pair of geckos in the colored boxes, a color volume overlap (CVO) is shown relative to its position in the tetrahedral color space defined by the visual system of avian predators and magnified in colored and black boxes; colors correspond to sites in the map coded by ecosystem and black boxes to random combinations of pictured geckos from different ecosystems. Note that males from the same ecosystem may differ considerably in coloration, but differences are typically greater between ecosystems.

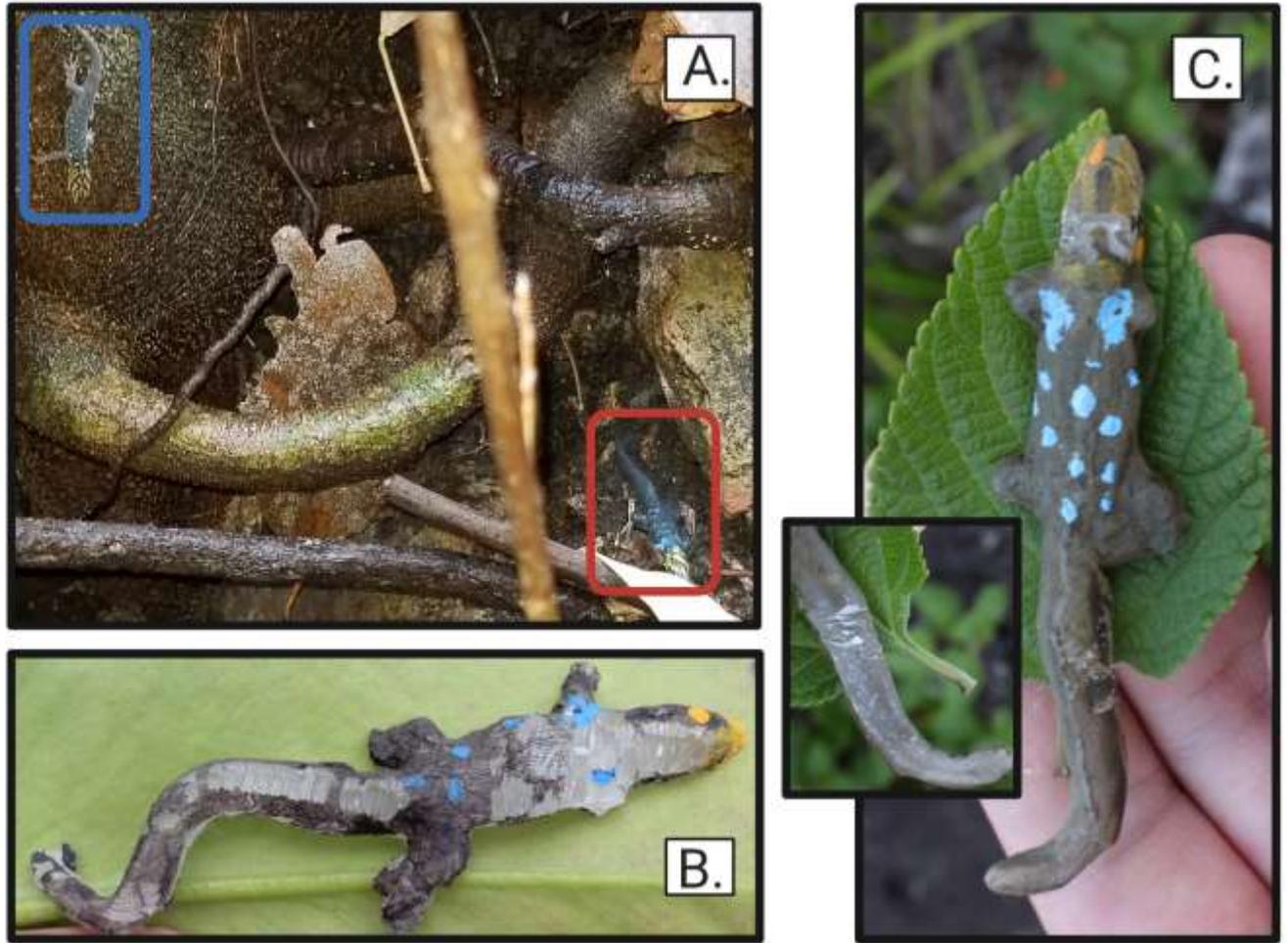


Figure 2. (A.) Male gecko (in blue) spotted approaching one of the paraffin models (in red) we placed in the field to measure predation pressure; note the resemblance between the live animal and the model. (B.) A model covered by bite marks indicating that a rodent was apparently more interested in scrapping the paint off rather than in preying upon the model. (C.) A model with a beak mark in the head and another in the base of the tail, showing evidence of a predation attempt by a bird.

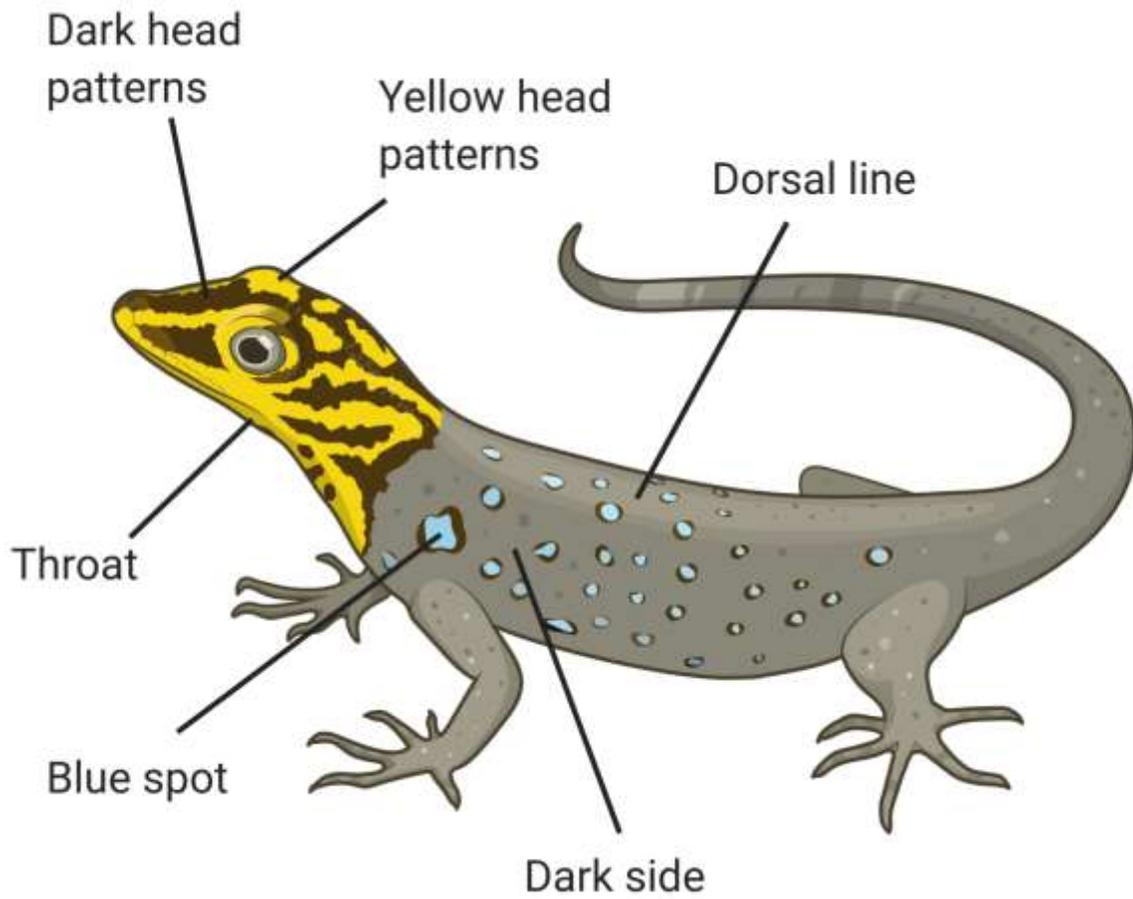


Figure 3. Illustration of a male *G. caudiscutatus* showing all color patches measured in this study and the nomenclature we employed. In females we only measured head patterns, dark sides, and dorsal lines.

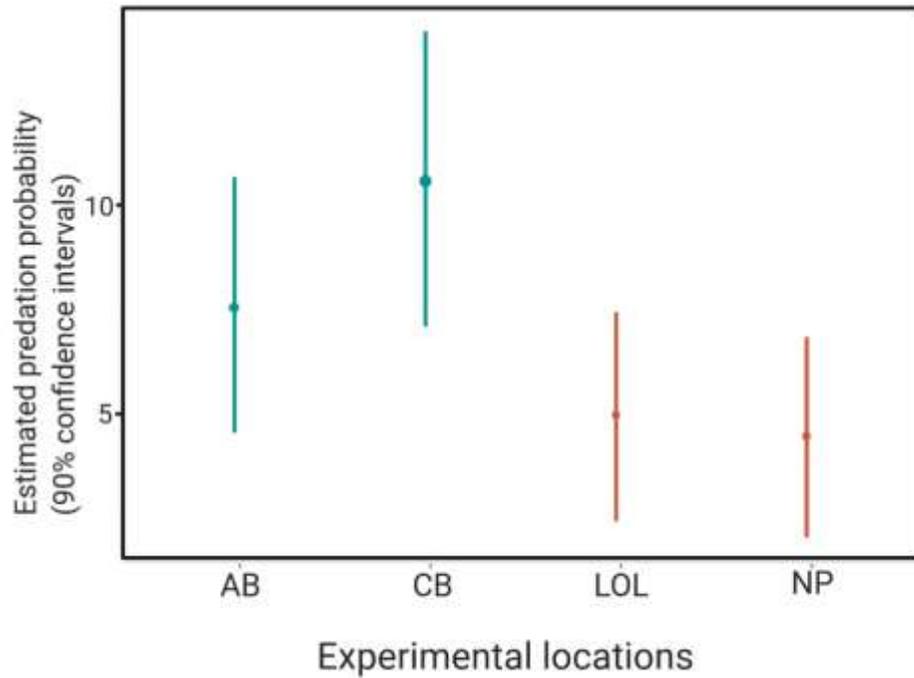


Figure 4. Continental populations (green) of *C. caudiscutatus* appear to be under stronger predation pressure than insular ones (orange). The figure shows predicted predation probabilities of paraffin models placed at each location along with 90% confidence intervals. AB = Agua Blanca, CB = Cerro Blanco, LOL = Lab of Life, NP = Galapagos National Park.

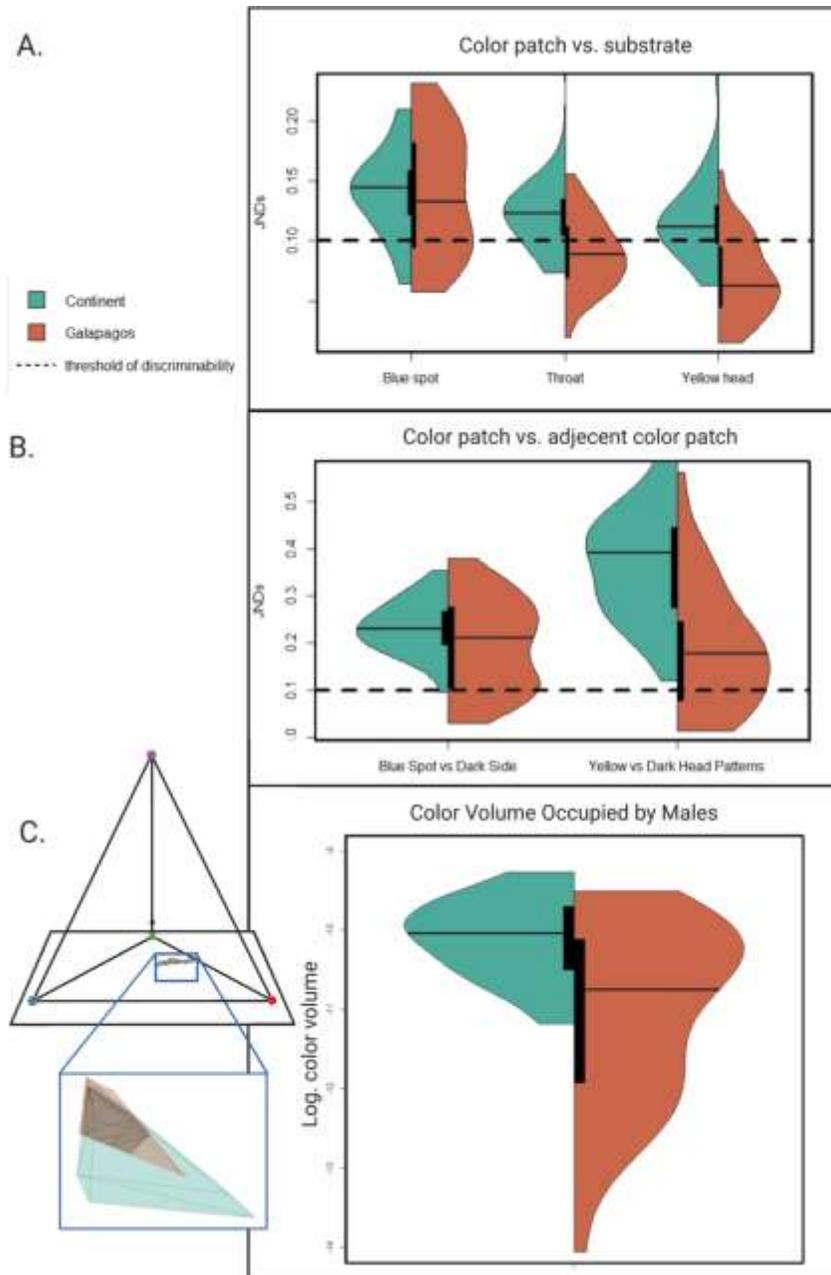


Figure 5. Split violin plots showing that continental male geckos (green) have more contrasting yellow head patterns, throats and blue spots, and are more colorful overall than insular ones (orange). In A, the dotted line represents the just-noticeable-difference (JND) threshold of discernibility between different color patches and the gecko's background given an avian visual model. In B the line represents this same JND threshold but comparing adjacent color patches in each male. The split violin in C shows that the color volume occupied in the tetrahedral color space defined by predator vision (C left) by continental male geckos is larger than the one occupied by their insular counterparts, Magnified an example of the comparison between a random continental and insular pair of males.



Figure 6. Two males of *G. caudiscutatus* captured in San Cristobal island showing how a lateral view of its head color patterns seem very conspicuous, but a dorsal view of the same patterns might work as a disruptive coloration with its environment.

Table 1. Results from ANOVAs showing continental males have yellow head patterns and throats which are significantly more contrasting with the substrate and with adjacent color patches than insular ones. In addition, continental males occupy larger volumes in color space. Significant p-values are shown in bold.

<b>Color patch vs substrate</b>	<i>R-square</i>	<i>df</i>	<i>F-statistic</i>	<i>p-value</i>
Yellow head patterns	0.3208	65	32.17	<b>&lt;0.0001</b>
Throat	0.2061	60	19.43	<b>&lt;0.0001</b>
Blue spot	-0.01005	69	0.304	0.5834
<b>Color patch vs adjacent color patch</b>				
Yellow head vs dark head patterns	0.2974	65	28.93	<b>&lt;0.0001</b>
Blue spot vs dark side	0.06413	64	5.454	<b>0.02267</b>
<b>Color volume</b>				
Males	0.2008	68	18.34	<b>&lt;0.0001</b>

Table 2. Results from Mixed Lineal Models showing continental males have yellow head patterns and throats which are significantly more contrasting with the substrate as well as blue spots and yellow head patterns more contrasting with adjacent colors than insular ones. In addition, continental males occupy larger volumes in color space. Significant p-values are shown in bold.

<b>Color patch vs substrate</b>	<i>Marginal R-square</i>	<i>Conditional R-square</i>	<i>Beta</i>	<i>Standard Beta</i>	<i>p-value</i>
Yellow head patterns	0.19	0.29	-0.57	-1.05	<b>&lt;0.01</b>
Throat	0.21	0.60	-0.34	-0.88	<b>&lt;0.0001</b>
Blue spot	0.01	0.22	-0.07	-0.20	0.53
<b>Color patch vs adjacent color patch</b>					
Yellow head vs dark head patterns	0.23	0.42	-1.06	0.59	<b>0.02</b>
Blue spot vs dark side	0.13	0.27	0.37	-0.75	<b>0.01</b>
<b>Color volume</b>					
Males	0.18	0.43	-0.88	-0.87	<b>0.02</b>