

Article

Visual “playback” of colorful signals in the field supports sensory drive for signal detectability

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Handling editor: Becky Fuller

Received on 1 February 2018; accepted on 2 June 2018

Abstract

Colorful visual signals are important systems for investigating the effects of signaling environments and receiver physiology on signal evolution as predicted by the sensory drive hypothesis. Support for the sensory drive hypothesis on color signal evolution is mostly based on documenting correlations between the properties of signals and habitat conditions under which the signals are given (i.e., a correlational approach) and less commonly on the use of mathematical models that integrate representations of visual environments, signal properties, and sensory systems (i.e., a functional approach). Here, we used an experimental approach in the field to evaluate signal efficacy of colorful lizard throat fans called dewlaps that show geographic variation in the lizard *Anolis cristatellus*. We used a remote controlled apparatus to display “fake dewlaps” to wild lizards to test for adaptive divergence in dewlap brightness (i.e., perceived intensity) among populations *in situ*. We found evidence of local adaptation in dewlap brightness consistent with the sensory drive hypothesis. Specifically, dewlaps that had the brightness characteristics of local lizards were more likely to be detected than those with the brightness characteristics of non-local lizards. Our findings indicate that simplified mathematical representations of visual environments may allow robust estimates of relative detectability or conspicuousness in natural habitats. We have shown the feasibility of evaluating color signal efficacy experimentally under natural conditions and demonstrate the potential advantages of presenting isolated components of signals to an intended receiver to measure their contribution to signal function.

Key words: Anolis, color signal, sensory drive, signal evolution.

Animals communicate with an amazing diversity of signals, and understanding the mechanisms that have favored this diversity has become a central theme in behavioral and evolutionary ecology. One hypothesis that has received considerable attention predicts that signal diversity is generated by selection for efficacy of communication, a process known as “sensory drive” (e.g., Endler 1992, 1993; Endler and Basolo 1998; Boughman 2002; Seehausen et al. 2008; Crampton et al. 2011; Price 2017). Sensory drive assumes that there is natural selection for signals to effectively stimulate the receiver sensory system and that the nature of the most effective

signal design depends on habitat conditions. Under this scenario, signal diversity evolves because species or populations come to occupy different habitat conditions where selection for effective communication promotes divergence in signal designs. Furthermore, adaptations for efficacy of communication (i.e., ability of the signal to effectively carry out its function) in one environment comes at the cost of decreased efficacy in another environment (Endler 1992).

Since it was presented by Endler and McLellan (1988), sensory drive has been implicated in local adaptation in signal design among populations as well as signal divergence between species, with

implications for selection and speciation (Leal and Fleishman 2004; Seehausen et al. 2008; Jacobs et al. 2017). Three approaches have been used to demonstrate that signals have evolved in accordance with sensory drive. The most common approach is correlational, in which studies document a relationship between the properties of signals and the local conditions under which the signals are given (e.g., Marshall 2000; Gomez and Théry 2007; Derryberry 2007; Ng et al. 2013; Derryberry et al. 2018). A second and less common approach is to model signal efficacy by integrating quantitative estimates of the signaling environment, signal form, and physiological or behavioral mechanisms of signal detection to infer signal performance under natural conditions, i.e., functional approach (e.g., Fleishman et al. 1997, 2009; Leal and Fleishman 2004; Endler et al. 2005; Cummings 2007; Stuart-Fox, et al. 2007; Uy and Stein 2007). The third approach, which is rarely used, is to experimentally measure the efficacy of the signal under natural conditions, i.e., experimental approach (Marchetti 1993).

Studies of visual signals using correlational and functional approaches have provided extensive evidence that selection can favor the evolution of physical signal properties that resist degradation as they travel through the environment and/or stand out against natural background “noise” (e.g., Endler and Théry 1996; Uy and Endler 2004; Endler and Mielke 2005; Cummings 2007; Doucet et al. 2007; Stuart-Fox, et al. 2007; Ng et al. 2013). Furthermore, studies using correlational and functional approaches have provided compelling evidence for local adaptation of signal spectral properties (i.e., color and brightness) to the spectral characteristics of the habitat (e.g., Leal and Fleishman 2002; Uy and Endler 2004; Gomez and Théry 2007; Seehausen et al. 2008). In general, this evidence supports the prediction that selection has favored the evolution of signal properties that allow the signal to be detected by the sensory system [i.e., signal efficacy (Guilford and Dawkins 1991; Dawkins and Guilford 1997)]. Efficacy is calculated in inference models by predicting the probability of detection of a signal under natural conditions based on the differences between the signal and the background in perceptual (color or brightness) space. This distance has been estimated based on Euclidian distances in chromaticity (or brightness) (Fleishman and Persons 2001; Stuart-Fox et al. 2007; Fleishman et al. 2016), or with models based on receptor noise (Vorobyev and Osorio 1998; Siddiqi et al. 2004; Endler and Mielke 2005; Kemp et al. 2015). Both types of models can provide accurate predictions of the role of stimulus/background contrast in signal detectability (Kemp et al. 2015; Fleishman et al. 2016). However, their predictions are rarely tested experimentally.

The most convincing way to determine if a signal is locally adapted is to experimentally measure its efficacy under natural conditions with free-living organisms. This can be done by conducting experiments in which multiple variants of the signal are presented in the wild and the response of intended receivers to those signals is measured. These experiments “ask” receivers if they detect the signal and if the different variants of the signal have the same detectability. A major advantage of the field approach is that it allows for signal efficacy to be assessed under complex visual conditions that are difficult to replicate in the laboratory, including the patchiness of the spectral environment, the quality and intensity of light, overall habitat noise due to the presence of other environmental distractors (e.g., stimulation within other sensory modalities and the presence of con- and heterospecifics) and their respective interactions. This “playback” framework has been used effectively to study acoustic signal evolution for decades (see Bretagnolle and Robinson 1991; Searcy et al. 1981; Schwartz 1993; Gerhardt et al. 2000; Römer et al.

2010; Preininger et al. 2013 and references therein), but this approach has only been applied to visual signals relatively recently (Ord and Stamps 2009; Macedonia et al. 2013; Klomp et al. 2017).

Here, we use a “playback” framework conducted under natural conditions to test for detection-driven local adaptation of dewlap (throat fans) coloration among populations of the lizard *Anolis cristatellus*. These lizards inhabit both open xeric and shaded mesic forests and exhibit differences in the spectral properties of the dewlap correlated with habitat types (Leal and Fleishman 2004). The xeric habitat is a desert scrubland with a mosaic of shaded patches under low trees. In contrast, the mesic habitat has a high continuous canopy with only small infrequent gaps.

Leal and Fleishman (2004) used a model of perceptual distance in chromatic and brightness space and behavioral experiments in the laboratory (Fleishman and Persons 2001), which can be described by the following equation:

$$P = 0.40[\text{ABS}(C_B)] + 0.43(C_C) = 0.16$$

where P = probability of detection and $\text{ABS}(C_B)$ = the absolute value of brightness contrast and C_C = chromatic contrast (please see Leal and Fleishman 2004 for detailed discussion of each parameter) to evaluate if population differences in dewlap spectral properties have resulted from selection to increase dewlap detectability under local habitat conditions via sensory drive. They found that xeric-habitat dewlaps are more detectable under xeric habitat conditions than under mesic habitat conditions, and mesic dewlaps are more detectable under mesic habitat conditions than under xeric habitat conditions. Furthermore, the model predicts that differences in dewlap detectability are primarily due to differences in brightness contrast between the two types of dewlaps (Leal and Fleishman 2004). Brightness contrast results from the differences between the perceived brightness of the stimuli and the background (Fleishman and Persons 2001). Importantly, the results of Leal and Fleishman (2004) do not predict that the brightest signals are the most detectable: mesic dewlaps are predicted to be most detectable in the mesic habitat because they should appear bright relative to the dark shaded background, but xeric dewlaps should be most detectable in the xeric habitat because they appear dark against the bright open background. To validate the prediction of the functional model that brightness differences between dewlaps are locally adapted, we created artificial dewlaps that match the brightness properties of real dewlaps from each habitat type. We then presented those dewlaps to free ranging *A. cristatellus* and compared the probability of detection of each artificial dewlap type within each habitat type. By presenting the artificial dewlaps, that produced similar brightness stimulation to those of real dewlaps under natural conditions, we were able to directly test the contribution of brightness contrast to the detection of the signals.

Materials and Methods

Field experiments were conducted from 08:00–17:00 h at a xeric site, Bosque Estatal de Aguirre ($N=143$) and a mesic site, Bosque Estatal de Cambalache ($N=133$) located on the island of Puerto Rico. For descriptions of the sites and light environments, see Leal and Fleishman (2004). The coloration of fake dewlaps was achieved by using an airbrush to paint white filter paper with grey or black water color and yellow (similar to real dewlaps) turmeric-based plant extract. The reflectance and transmission of each fake dewlap was measured following the methodology of Leal and Fleishman (2004). In short, a light source, (Mille Luce M 1000) was pointed to a large sheet of tracing paper to create a broad circle of diffuse light

to illuminate the fake dewlap. The fake dewlap was positioned at the center of this circle at a distance of ~ 15 cm. To measure reflectance, the radiance probe of an Ocean Optics USB 2000 spectroradiometer was positioned on the same side of the fake dewlap as the light source and was pointed at the fake dewlap at an angle of $\sim 70^\circ$. To measure transmission, the probe was placed on the opposite side of the fake dewlap. After each set of fake dewlap radiance measurements was completed, we measured the spectral irradiance of the light striking the front of the fake dewlap using a cosine-corrected irradiance probe placed at the position where the dewlap was placed during the measurements. For representative radiance/irradiance spectra, see [Supplementary Figure S1](#).

Brightness perception in *Anolis* is achieved through stimulation of the long-wavelength sensitive (LWS) double-cone (Fleishman et al. 1997; Persons et al. 1999), which in *A. cristatellus* is sensitive from ~ 450 – 700 nm (Loew et al. 2002; Leal and Fleishman 2002). To determine if fake dewlaps adequately matched the spectral properties of a real dewlap from the lizard's perspective, we used data of the visual physiology of *A. cristatellus* (Fleishman et al. 1997; Persons et al. 1999; Leal and Fleishman 2002) to model retinal stimulation of a lizard observing the fake dewlap under mean diurnal light conditions in each habitat using the equation:

$$\text{retinal stimulation} = \sum \left[\left(\frac{\text{fake dewlap reflection radiance/irradiance}}{\text{habitat irradiance}} + \frac{\text{fake dewlap transmission radiance/irradiance}}{\text{habitat irradiance}} \right) \times \text{retinal sensitivity} \right]$$

from 450 – 700 nm, with retinal sensitivity from an electroretinogram (ERG) of *A. cristatellus* (Leal and Fleishman 2004). Those values were then compared to values of retinal stimulation predicted for real dewlaps under the same conditions. A fake dewlap was designated an adequate match for a real dewlap if its retinal stimulation in each habitat was within 5% of the retinal stimulation of the real dewlap type it was supposed to mimic (Figure 1).

Probability of detection

We used the “visual grasp reflex” to evaluate if the fake dewlap was effective at eliciting the attention of a lizard. The visual grasp reflex results from the image of an object with particular motion characteristics traveling across the peripheral retina of an organism, eliciting a shift in gaze (Fleishman 1992). The visual grasp reflex was used to evaluate the probability that *A. cristatellus* detected a dewlap like stimulus under laboratory conditions (Fleishman and Persons 2001) and is commonly used to evaluate the efficacy of visual signals (Fleishman 1986; Steinberg and Leal 2013, 2016). In the case of anoles, a stimulus is considered effective at eliciting attention if it elicits a shift in gaze which foveates the stimuli, thereby focusing an individual's direct attention on it (Fleishman 1986; Fleishman and Persons 2001).

Fake dewlaps were presented to lizards using a remote-controlled apparatus that mimics an anole giving a dewlap display while perched on a horizontal branch (Figure 2). Each fake-dewlap display lasted approximately 2 s: 1 s from initiation of movement to maximum amplitude, and 1 s for the retraction of the dewlap. The display was controlled using the proportional “wheel” channel of a two-channel radio transmitter. Presentations were made to adult lizards found while walking transects in each habitat, with a different transect used each day to avoid presenting to the same animals. A compass was used to place the dewlap display apparatus at either 25° (to the left) or 335° (to the right) with respect to the sagittal plane of the lizard at a distance of ~ 3 m ([Supplementary Figure S2](#)).

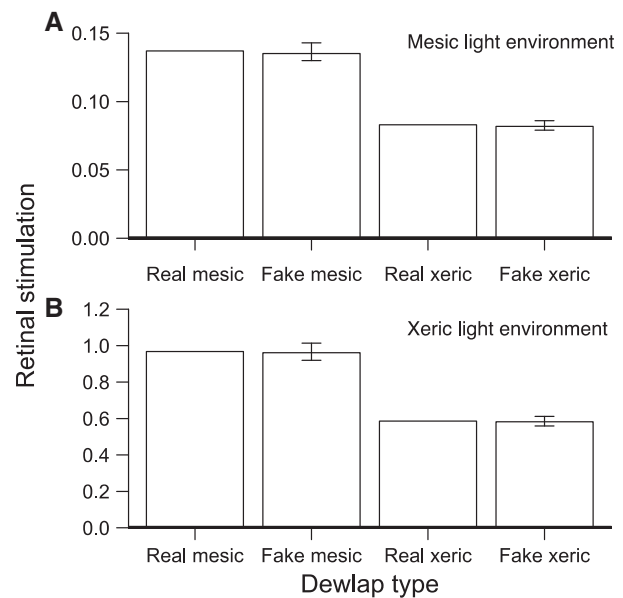


Figure 1. Predicted double-cone stimulation of a lizard viewing mean real dewlaps and the fake dewlaps used in this study. (A) In mesic habitat. (B) In xeric habitat. Error bars denote the range. Note differences in y-axis scale.



Figure 2. Dewlap display apparatus. (A) Acrylic box within which electrical components were placed. The rule next to the box is 15.25 cm in length. (B) Electrical components inside the acrylic box with a fake dewlap displayed. (C) The apparatus in the field with a fake dewlap displayed.

The observer then moved to 90° (or 270°) at a distance of ~ 4 m and waited motionless for 60 seconds, then waived a hand in the air to draw the attention of the lizard to the observer. This ensured that the fake dewlap apparatus was in the periphery of the visual field of the focal animal. After five seconds, the fake dewlap was displayed and the observer recorded the response of the lizard. We considered any shift in gaze via eye or head movement by a lizard towards the stimulus within four seconds of the end of dewlap display as a positive response (*i.e.*, an indication of stimulus detection), and the absence of a gaze shift as a negative response. If the lizard did not respond after this first display, the observer waited another five seconds and presented the fake dewlap a second time. We also conducted control trials in which the exact methods outlined above were used, but there was no fake dewlap attached to the apparatus. In the mesic habitat, we conducted $N = 54$ trials with the mesic fake dewlap, $N = 53$ trials with the xeric fake dewlap, and $N = 26$ control trials. In the xeric habitat, we conducted $N = 57$ trials with the

mesic fake dewlap, $N=58$ trials with the xeric fake dewlap, and $N=28$ control trials.

Generalized linear models with binomial error (Zuur et al. 2009) were applied to assess lizard responses to fake dewlaps using the *glm* function in R (R development core team, 2012). We first tested for a significant interaction between habitat and dewlap type using an analysis of deviance test to compare models with and without the interaction term. This test was conducted using the *anova* function, and the interaction was significant ($P=0.007$). After confirming the significant interaction between habitat and dewlap type, we conducted one-tailed planned orthogonal contrasts to test the hypothesis that each dewlap type had greater detectability in its native habitat relative to the non-native dewlap type. We applied one-tailed tests because we had *a priori* expectations that each dewlap type would be more detectable in its native habitat than the non-native dewlap type (Leal and Fleishman 2004). Control trials were excluded from analyses, though the data are presented for heuristic purposes.

Results

Lizards in the mesic habitat detected fake dewlaps that mimicked the dewlaps of mesic lizards more often than they detected fake dewlaps that mimicked the dewlaps of xeric lizards ($P=0.015$; Figure 3). In the xeric habitat the pattern was reversed, with a higher response to fake dewlaps that mimicked the dewlaps of xeric lizards, although the difference did not reach significance ($P=0.068$).

Discussion

Sensory drive has long been seen as a powerful evolutionary force shaping the evolution of animal color signals (Endler 1992, 1993; Boughman 2002; Mann and Seehausen 2011; Price 2017). However, experimental evidence supporting the predictions sensory drive hypothesis is relatively rare. To help bridge this gap, we presented free-ranging *A. cristatellus* with fake dewlaps that mimic geographic variation in dewlap signal properties predicted to influence signal detectability. Our findings support the sensory drive hypothesis and strongly suggest that the brightness properties of *A. cristatellus* dewlaps are locally adapted via selection on signal efficacy. Within each habitat type, individuals were more likely to detect fake dewlaps that matched the brightness properties of resident dewlaps than fake dewlaps that matched the brightness properties of non-resident dewlaps. These results highlight the utility and feasibility of using a field “playback” design to test hypotheses regarding color signal evolution under natural conditions.

In the darker, shaded mesic habitat, lizards responded to fake dewlaps that matched the brightness characteristics of mesic habitat dewlaps nearly twice as often as they responded to fake dewlaps that matched the brightness of xeric habitat dewlaps (Figure 3). Mesic habitat dewlaps are “brighter” than xeric habitat dewlaps, and thus appear bright against the dark, shaded mesic forest background. We found a similar trend in the xeric habitat, where lizards responded to the xeric fake dewlap nearly twice as often as the mesic fake dewlap, although this pattern did not quite reach significance because overall detection levels were lower (Figure 3). Xeric habitat dewlaps have relatively low reflectance and transmission, and should thus appear relatively dark against the bright xeric background (Leal and Fleishman 2004).

We found overall support for sensory drive despite the complexity of the terrestrial light environment (Endler 1993; Fleishman et al. 2009). Nonetheless, the low overall detection rates in the xeric

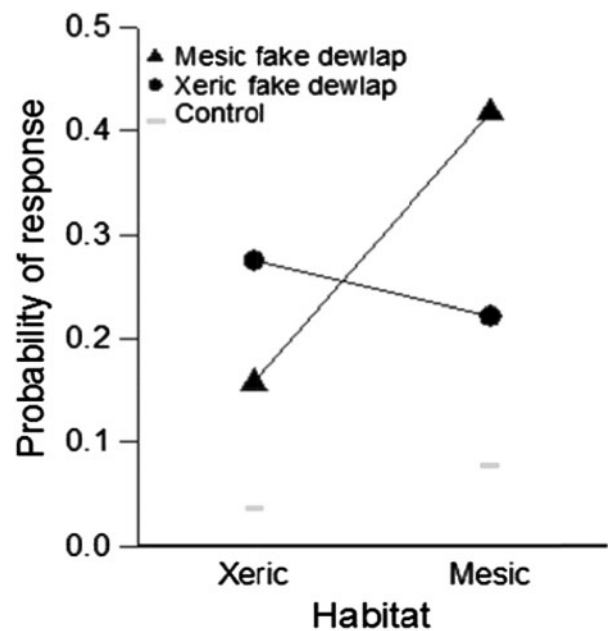


Figure 3. Response of free-ranging *A. cristatellus* to fake dewlaps that mimic the achromatic properties of real dewlaps.

habitat were not predicted by the initial functional model of dewlap detectability (Leal and Fleishman 2004) and may relate to the fact that the xeric habitat is a much more heterogeneous visual environment (see Supplementary Figure S3). The xeric habitat is a desert scrubland with shaded patches under low trees interspersed with open patches of bare ground, low shrubs, and grasses. In contrast, the mesic habitat has a high, continuous canopy with only small infrequent gaps. These differences might result in differences in the degree of brightness patchiness within each of the habitats. Spatial variation in habitat light conditions can reduce the overall efficacy of signals in at least two different ways. First, the xeric habitat likely has greater contrast between background elements compared to the mesic habitat, increasing background noise. Second, the detectability of the signal will change greatly depending on where the signaler and receiver are positioned. Thus, for signals like dewlaps with fixed physical properties, it may be difficult to evolve spectral characteristics that are effective over the range of environmental light conditions experienced. This effect could be reduced if signalers non-randomly select display localities within the forest (e.g., Endler and Thery 1996; Heindl and Winkler 2003; Uy and Endler 2004); however, *A. cristatellus* does not engage in this type of behavior (Fleishman et al. 2009).

The response of *A. cristatellus* to the presentation of dewlap-like stimulus was similar to those recorded under the laboratory conditions (Persons et al. 1999), despite the presence of potential sources of background noise and distractions present under the conditions of this experiment (e.g., conspecifics, heterospecific anoles, predators, prey). This finding underlines the salience of the dewlap as a visual signal.

Our experiments under field conditions indicate that models of visual signal detectability can provide reliable estimates of signal efficacy in nature. In addition, they support the hypothesis that evolution for achromatic contrast may be an important target for selection on visual signals. However, the lower overall detection in the xeric habitat suggests that, as visual environments become more

complex, laboratory-based models of detectability may become less effective at assessing absolute detection levels and field-based approaches may be warranted.

An important aspect of our experimental design is that our apparatus for displaying the fake dewlaps did not resemble a lizard in any way. Signals that function to communicate the presence of an individual, such as the dewlap of anoles, are predicted to do so even when the signaler cannot be clearly seen by the receiver (Fleishman et al. 2016). In other words, selection should favor the evolution of signals for which only the display of the signal should be sufficient to elicit the response from the receiver. In anoles and many other taxa, multiple additional aspects of a signaler's morphology and behavior might also serve as signals, such as body position, body coloration, motion, and size (Rand and Williams 1970). This multitude of possible signals can confound any interpretations of experiments that manipulate the signal of interest, but leave all other signals present. Individuals of *A. cristatellus* responded to “fake-dewlaps” even though no other cues were available, which strongly supports the function of the dewlap as a signal to capture the attention of a receiver. Furthermore, the finding that individuals were more likely to respond to fake dewlaps from their own population opens the possibility that the brightness component of the dewlap could contribute to a species recognition function of this signal.

Over the last two decades, studies evaluating the potential role of sensory drive in driving signal evolution have flourished (see papers cited in the introduction and those published as part of this issue). Our findings and those presented by Klomp et al. (2017) illustrate both the feasibility of using “playbacks” to evaluate the function of visual signals under natural conditions, and the robustness of this approach for elucidating whether signals are locally adapted. We encourage future studies in other systems to explore the possibility of using the approach described in this paper. Systems in which multiple approaches are used to test the predictions of the sensory drive hypothesis are likely to provide the best insights into the interactions between the sensory system, signal design and habitat conditions and how those interactions shape signal evolution. For example, in the case of anoles, results from a series of studies at the population and community level using different approaches (Leal and Fleishman 2004; Ng et al. 2013) are beginning to shed light on the possibility that dewlap coloration is locally adapted, as predicted by sensory drive. Furthermore, evidence suggests that the chromatic and achromatic components of the dewlaps are under selection to increase detectability and also to facilitate discrimination between sympatric species (Leal and Fleishman 2004; Fleishman et al. 2009). The latter is not a prediction of sensory drive, and might account for the observation that in some instances dewlaps don't exhibit an optimal design for detectability (Fleishman et al. 2009; Macedonia et al. 2014).

Finally, our findings show that estimation of signal detectability based on models for which data on the sensory system, spectral properties of the signal, and spectral properties of signaling environment are known can be relatively robust. The generality of our findings to other systems remains an open question, and one that should be addressed, to develop a better understanding of the potential similarities and differences between sensory systems and the efficacy of communication under natural conditions.

Acknowledgments

We thank the Chipoyo Lab reading group for helpful comments on this article. We are grateful to the Departamento de Recursos Naturales y Ambientales de

Puerto Rico (2012-IC-065), which provided all the necessary permits for conducting fieldwork.

Funding

Funding was provided by a student research grant from the Animal Behavior Society to A.R.G. and a grant from the National Science Foundation (IOS-1051793) to M.L.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

Author Contributions

A.R.G. and M.L. conceived and designed the study. A.R.G. collected and analyzed the data. A.R.G., M.L., and L.J.F. contributed to the preparation of the article.

References

- Boughman JW, 2002. How sensory drive can promote speciation. *Trends Ecol Evol* 17:571–577.
- Bretagnolle V, Robinson P, 1991. Species-specific recognition in birds: an experimental investigation of Wilson's storm-petrel (Procellariiformes, Hydrobatidae) by means of digitalized signals. *Can J Zool* 69:1669–1673.
- Crampton WGR, Lovejoy NR, Waddell JC, 2011. Reproductive character displacement and signal ontogeny in a sympatric assemblage of electric fish. *Evolution* 65:1650–1666.
- Cummings ME, 2007. Sensory trade-offs predict signal divergence in surfer perch. *Evolution* 61:530–545.
- Dawkins MS, Guilford T, 1997. Conspicuousness and diversity in animal signals. *Perspectives in Ethology* 12:55–75.
- Derryberry EP, 2007. Evolution of bird song affects signal efficacy: an experimental test using historical and current signals. *Evolution* 61:1938–1945.
- Derryberry EP, Seddon N, Derryberry GE, Claramunt S, Seeholzer GF et al., 2018. Ecological drivers of song evolution in birds: disentangling the effects of habitat and morphology. *Ecol Evol* 8:1890–1905.
- Doucet SM, Mennill DJ, Hill GE, 2007. The evolution of signal design in manakin plumage ornaments. *Am Nat* 169:S62–S80.
- Heindl M, Winkler H, 2003. Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. *Biol J Linn Soc* 80:647–658.
- Endler JA, 1992. Signals, signal conditions, and the direction of evolution. *Am Nat* 139:S125–S153.
- Endler JA, 1993. The color of light in forests and its implications. *Ecological Monographs* 63:1–27.
- Endler JA, McLellan T, 1988. The processes of evolution: toward a newer synthesis. *Annu Rev Ecol Syst* 19:395–421.
- Endler JA, Basolo AL, 1998. Sensory ecology, receiver biases and sexual selection. *Trends Ecol Evol* 13:415–420.
- Endler JA, Thery M, 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am Nat* 148:421–452.
- Endler JA, Mielke PW, 2005. Comparing entire colour patterns as birds see them. *Biol J Linn Soc* 86:405–431.
- Endler JA, Westcott DA, Madden JR, Robson T, 2005. Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution* 59:1795–1818.
- Fleishman LJ, 1986. Motion detection in the presence and absence of background motion in an *Anolis* lizard. *J Comp Physiol A* 159:711–720.
- Fleishman LJ, 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am Nat* 139:S36–S61.

- Fleishman LJ, Persons M, 2001. The influence of stimulus and background colour on signal visibility in the lizard *Anolis cristatellus*. *J Exp Biol* 204: 1559–1575.
- Fleishman LJ, Leal M, Persons M, 2009. Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *J Comp Physiol A* 195: 1043–1060.
- Fleishman LJ, Bowman M, Saunders D, Miller W, Rury M et al., 1997. The visual ecology of Puerto Rican anoline lizards: habitat light and spectral sensitivity. *J Comp Physiol A* 181:446–460.
- Fleishman LJ, Ogas B, Steinberg D, Leal M, 2016. Why do *Anolis* dewlaps glow? An analysis of a translucent visual signal. *Funct Ecol* 30:345–355.
- Gerhardt HC, Roberts JD, Bee MA, Schwartz JJ, 2000. Call matching in the quacking frog *Crinia georgiana*. *Behav Ecol Sociobiol* 48:243–251.
- Gomez D, Théry M, 2007. Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a neotropical rainforest bird community. *Am Nat* 169:S42–S61.
- Guilford T, Dawkins MS, 1991. Receiver psychology and the evolution of animal signals. *Anim Behav* 42:1–14.
- Jacobs DS, Catto S, Mutumi L, Finger N, Webala PW, 2017. Testing the sensory drive hypothesis: geographic variation in echolocation frequencies of Geoffroy's horseshoe bat (*Rhinolophidae: rhinolophus clivosus*). *PLoS One* 12:e0187769.
- Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD et al., 2015. An integrative framework for the appraisal of coloration in nature. *Am Nat* 185:705–724.
- Klomp DA, Stuart-Fox D, Cassidy EJ, Ahmad N, Ord TJ, 2017. Colour pattern facilitates species recognition but not signal detection: a field test using robots. *Behav Ecol* 28:597–606.
- Leal M, Fleishman LJ, 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proc Roy Soc Lond B* 269:351–359.
- Leal M, Fleishman LJ, 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *Am Nat* 163:26–39.
- Loew ER, Fleishman LJ, Foster RG, Provencio I, 2002. Visual pigments and oil droplets in diurnal lizards a comparative study of Caribbean anoles. *J Exp Biol* 205:927–938.
- Macedonia JM, Clark DL, Riley RG, Kemp DJ, 2013. Species recognition of color and motion signals in *Anolis grahami*: evidence from responses to lizard robots. *Behav Ecol* 24:846–852.
- Macedonia JM, Clark DL, Tamasi AL, 2014. Does selection favor dewlap colors that maximize detectability? A test with five species of Jamaican *Anolis* lizards. *Herpetologica* 70:157–170.
- Mann ME, Seehausen O, 2011. Ecology, sexual selection and speciation. *Ecol Lett* 14:591–602.
- Marchetti K, 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362:149–152.
- Marshall NJ, 2000. Communication and camouflage with the same “bright” colours in reef fishes. *Proc Roy Soc Lond B* 355:1243–1248.
- Ng J, Landeen EL, Logsdon RM, Glor RE, 2013. Correlation between *Anolis* lizards dewlap phenotype and environmental variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution* 67:573–582.
- Ord TJ, Stamps JA, 2009. Species identity cues in animal communication. *Am Nat* 174:585–593.
- Persons M, Fleishman LJ, Frye M, Stimpfl M, 1999. Sensory response patterns and the evolution of visual signal design in anoline lizards. *J Comp Physiol A* 184:585–607.
- Price TD, 2017. Sensory drive, color and color vision. *Am Nat* 190:157–170.
- Preininger D, Boeckle M, Szatecsny M, Hödl W, 2013. Divergent receiver responses to components of multimodal signals in two foot-flagging frog species. *PLoS One* 8:e55367.
- R Core Team, 2012. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Rand SA, Williams EE, 1970. An estimation of redundancy and information content of anole dewlap. *Am Nat* 104:99–103.
- Römer H, Lang A, Hartbauer M, 2010. The signaller's dilemma: a cost-benefit analysis of public and private communication. *PLoS One* 5:e13325.
- Schwartz JJ, 1993. Male calling behavior, female discrimination and acoustic interference in the Neotropical Treefrog *Hyla microcephala* under realistic acoustic conditions. *Behav Ecol Sociobiol* 32:1–414.
- Searcy WA, McArthur PD, Peters SS, Marler P, 1981. Responses of male song and swamp sparrows to neighbour, stranger, and self songs. *Behaviour* 77:152–163.
- Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K, 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J Exp Biol* 207:2471–2485.
- Seehausen O, Terai Y, Magalhaes IS, Carleton KL, Mrosso HD et al., 2008. Speciation through sensory drive in cichlid fish. *Nature* 455:620–626.
- Steinberg DS, Leal M, 2013. Sensory system properties predict signal modulation in a tropical lizard. *Anim Behav* 85:623–629.
- Steinberg DS, Leal M, 2016. Visual motion detection and habitat preference in *Anolis* lizards. *J Comp Physiol A* 202:783–790.
- Stuart-Fox D, Moussalli A, Whiting MJ, 2007. Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *Am Nat* 170:916–930.
- Uy JAC, Endler JA, 2004. Modification of the visual background increases the conspicuousness of golden-collared manakin displays. *Behav Ecol* 15: 1003–1010.
- Uy JAC, Stein AC, 2007. Variable visual habitats may influence the spread of colourful plumage across an avian hybrid zone. *J Evol Biol* 20:1847–1858.
- Vorobyev M, Osorio D, 1998. Receptor noise as a determinant of colour thresholds. *Proc Roy Soc Lond B* 265:351–358.
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM, 2009. *Mixed Effects Models and Extensions in Ecology with R*, New York, NY: Springer.