GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 15 (2014) 326–335
Basic and Applied Ecology
www.elsevier.com/locate/baae

# Characterizing background heterogeneity in visual communication

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Received 23 September 2013; accepted 4 June 2014
Available online 10 June 2014

## Abstract

How is a visual signal effectively transmitted through an environment triggering a response by a perceiver? Experimental and theoretical works in disparate fields, such as sexual selection and plant–animal interactions, have demonstrated selection based on signal conspicuousness. However, to properly describe the conspicuousness of a signal, it is necessary to quantify the spatial and temporal heterogeneity of background coloration of a signaler. We intend to compare the effectiveness of four methods developed to characterize background heterogeneity. To describe the background in a seasonal vegetation, we collected reflectance data in dry and wet seasons of (i) *target leaves* (those leaves against which a signal is predominantly displayed); (ii) *overall leaves* (leaves from the most common plant species in the community); (iii) *frames* in a limited area in space, by measuring the reflectance of all material found in the background; and (iv) background items from the most common species, based on their abundance along *transects*. We analyzed seasonal color changes in terms of hue, chroma and brightness and described the conspicuousness of fruit coloration according to avian vision. All methods found significant differences in the background coloration between seasons, with higher reflectance values in the dry season. Hue values were higher in the dry season, and chroma values were higher in the wet season. Only the methods most restricted in space (*target leaves* and *frames*) recorded seasonal differences in fruit conspicuousness. The *transects* and *frames* methods are useful for describing the backgrounds of non-stationary signals (i.e., those of most animals). For plant signals, which are displayed against a fixed background in space, we recommend specific sampling of *target leaves*. Our results support the importance of measuring the seasonal heterogeneity of the background but also indicate that a monthly sampling design is not necessary to evaluate the conspicuousness of fruit signals.

## Zusammenfassung

Was beeinflusst die Effektivität von visuellen Signalen, so dass sie eine Antwort von Empfängern auslösen? Experimentelle und theoretische Arbeiten in so unterschiedlichen Feldern wie sexueller Selektion und Pflanze-Tier Interaktionen haben eine

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http://dx.doi.org/10.1016/j.baae.2014.06.002

Selektion auf höhere Auffälligkeit von Signalen nachgewiesen. Um die Auffälligkeit von Signalen bestimmen zu können, ist es notwendig, die räumliche und zeitliche Heterogenität des Hintergrundes zu quantifizieren. Hier vergleichen wir vier Methoden, die die Heterogenität des Hintergrundes beschreiben. In einer saisonalen Flora haben wir Reflexionsdaten in der Trocken- und Regenzeit gesammelt, die (i) nur von den Blättern der Zielarten stammen, vor denen die Signale zu sehen sind; (ii) von allen häufigen Pflanzen der Busch- und Strauchschicht; (iii) von allen Hintergrundmaterialien, die an Zufallspunkten in der Umgebung von Fruchtständen gefunden wurden; (iv) von Hintergrundobjekten, die entlang von Transekten erhoben wurden. Wir haben saisonale Farbänderungen als Farbton, Sättigung und Helligkeit analysiert und außerdem die Auffälligkeit von Fruchtfarben für das Sehvermögen von Vögeln modelliert. Alle Methoden fanden saisonale Unterschiede in der Farbe des Hintergrundes. Die Farbtöne waren gelblich-grüner in der Trockenzeit und gesättigter in der Regenzeit. Nur die räumlich stark begrenzten Methoden i und iii fanden saisonale Unterschiede in der Fruchtauffälligkeit für Vögel. Für Pflanzensignale, die vor einem konstanten Hintergrund gesehen werden, bietet sich die Methode der Zielarten an. Unsere Studie belegt die Wichtigkeit die saisonale Heterogenität der Hintergründe zu beachten; sie zeigt auch dass eine monatliche Datenaufnahme von Reflexionsdaten nicht notwendig ist, um die Auffälligkeit von Fruchtsignalen zu evaluieren.


***Keywords:*** Signal; Camouflage; Cerrado savanna; Crypsis; Frugivory; Fruit color; Fruit contrast; Plant–animal interactions; Pollination; Seasonality

## Introduction

Visual communication can impact the survival and reproductive success of plants and animals (Ruxton, Sheratt, & Speed 2004; Schaefer & Ruxton 2011). The central question is: how is a visual signal effectively transmitted through an environment triggering a response by a perceiver? This question has become an important topic in studies on the evolutionary ecology of visual communication over the last several decades due to recent improvements in quantifying signals and their background and a better understanding of animal sensory spaces. However, this is not a new question. In 1895, Kerner formulated the contrast hypothesis, positing that fruits that stand out from their background are easily detected by frugivorous birds, thus increasing plant fitness due to the resultant high fruit removal rates. In addition, Cott (1940) described various adaptations that allow animals to conceal themselves depending on the background.

The predominant answer to what causes a visual signal to be effectively transmitted is a high signal-to-noise ratio (i.e., a strong contrast against the background) (Endler 1982; Schaefer & Ruxton 2011; Stevens 2013). Accordingly, experimental and theoretical works in disparate fields, such as sexual selection and plant–animal interactions, have demonstrated selection based on signal conspicuousness (Cazetta, Schaefer, & Galetti 2009; Delhey, Hall, Kingma, & Peters 2013). However, these and most other studies in the fields of evolutionary and behavioral ecology have quantified contrasts against either a single (e.g., Théry, Debut, Gomez, & Casas 2005; Schaefer, Schaefer, & Vorobyev 2007) or a mean background (e.g., Darst, Cummings, & Cannatella 2006; Stuart-Fox & Moussalli 2008). While this approach approximates how contrasts are selected, it oversimplifies the search task by ignoring the spatial heterogeneity and temporal variability in the background.

Heterogeneity in the background is important because targets are typically more difficult to detect against more complex backgrounds (e.g., those characterized by high contrasts between background items) (Dimitrova, Stobbe, Schaefer, & Merilaita 2009). This effect of background heterogeneity is consistent with the behavior of birds, such as manakins, that clean the leaf litter from their court arenas and thereby become more conspicuous against the cleaned court (Uy & Endler 2004). Visual systems include receptive fields that process natural scenes by breaking them down into distinct spatial scales (reviewed in Stevens 2007). Changes in the light intensity and composition play a key role in the differentiation between objects and the background. As such, background heterogeneity is important because it may distract perceivers from identifying targets correctly.

Although the importance of considering natural scenes – and, thus, the temporal and spatial patterns of background heterogeneity – is known, these factors are often neglected (Chiao, Cronin, & Osorio 2000; To, Lovell, Troscianko, & Tolhurst 2008). Therefore, it is unclear whether the heterogeneity commonly found in backgrounds is significant because it influences the perception of targets. In addition, it remains unclear whether fine-scale adaptations in terms of crypsis or conspicuousness (e.g., in moths [Endler 1984] and animal-dispersed fruits [Camargo, Cazetta, Schaefer, & Morellato 2013]) occur more widely.

Our aim was to propose and compare the effectiveness of four methods developed to characterize background heterogeneity in space and time to improve the understanding of interactions based on visual communication. Hence, we collected background reflectance data in a seasonal vegetation, the Brazilian cerrado savanna, and compared seasonal color changes in terms of hue, chroma and brightness, which are useful parameters for describing the seasonal phenology of plants (e.g., Camargo et al. 2013) or background