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The Polarization of Light in a Tropical Rain Forest[1]

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ABSTRACT

The light environment within forests presents complex patterns of brightness and spectral distribution of light. The polarized light field is no less complex. Using an imaging polarized light analyzer, we examined the natural fields of linearly polarized light in the tropical rain forest of Guatopo National Park, Venezuela. We found that the celestial polarization pattern remains visible underneath the forest canopy, although cloud and fog coverage may diffuse the light and reduce the polarization signal. We characterized several distinct light environments, each having a characteristic polarized light field. Furthermore, objects throughout the forest reflect light that is polarized in a predictable fashion depending upon the material, structure, and orientation of the reflecting surface. As a consequence of these patterns in the distribution of polarized light, some functions of polarization vision, such as navigation, must be limited to the spaces exposed to several extended portions of the sky, while others, such as remote sensing of surface orientation, object detection, and breaking of camouflage would be useful throughout the forest. The polarization of light adds another dimension to the complexity of the rain forest photic environment.

RESUMEN

La luz ambiental dentro de la jungla presenta complejos patrones de brillo y distribución espectral de luz. El campo de la luz polarizada no es menos complejo. Usando un analizador de imagenes de luz polarizada, nosotros examinamos los campos naturales de luz polarizada linear en el bosque tropical del Parque Nacional de Guatopo, Venezuela. Encontramos que el patrón de polarización celestial permanece visible debajo de la cubierta del bosque, aun cuando una cubierta de nubes y neblina puede dispersar la luz y reducir la señal de polarización. Nosotros caracterizamos varios ambientes de luz diferente, cada uno teniendo un campo de luz polarizada característico. Además, objetos en todo el bosque reflejan la luz que es polarizada en una forma predecible dependiendo sobre el material, estructura y orientación de la superficie reflectante. Como una consequencia de estos patrones en la distribución de la luz polarizada, algunas funciones de visión polarizada, tales como la navegación, deben estar limitadas a los espacios expuestos a grandes extensiones de cielo, mientra otras, tales como la percepción remota de la orientación de superficies, la detección de objetos, y el quebrantar el camuflage puede ser útiles dentro del bosque. La polarización de la luz adiciona otra dimensión a la complejidad del ambiente fótico del bosque.

Key words: natural light fields; photic environment; polarized light vision; sensory ecology.

Many characteristics of light carry distinct information that is sensed and utilized by visual systems of animals. Intensity, or the rate of photon arrival, is perceived as brightness. The wavelength distribution of the incoming light may be associated with hue. An additional characteristic of light that is sensed by numerous animals (but not by humans) is the state of partial polarization of light.

As is well known, light has a wave nature, in which every light beam is composed of many waves. When the planes of the magnetic and electrical fields of all waves in a light beam are parallel, the light is fully linearly polarized; when they are

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at random orientations to each other, the light is depolarized. While the relative orientations of the magnetic and electric fields may change through time, creating circular polarization, and combinations of circular and linear polarization in a light beam can produce elliptical polarization, in this paper we will consider only linear polarization. Variations in the extent to which the fields' planes of the waves are parallel will result in different levels of partial polarization (also termed degree, or percentage, of polarization). Partially linearly polarized light can be described as a mixture of two states, one completely depolarized, with an intensity of I_d, and the other fully linearly polarized having an intensity of I_p (Kliger *et al.* 1990). The angle of polarization (or the orientation of polarization) of partially linearly polarized light is defined as the dominant orientation of the *e*-vector (the spatial vector of the electrical field in the light beam). The intensity of the light, when measured using a perfect analyzer oriented perpendicular to the orientation of polarization, equals $I_d/2$. When examined at the orientation of polarization, the light intensity equals $I_d/2+I_p$, and the total intensity (I_t) can be described as: $I_t = I_d+I_p$. The partial polarization is defined as I_p/I_t, and it ranges from 0 to 1 (0%-100%) inclusive, where 0 indicates unpolarized, and 1 (or 100%) indicates fully polarized light (Wolff 1990).

The natural distribution of linearly polarized light in the sky, which arises from the scattering of light by molecules and small particles in the atmosphere (known as Rayleigh scattering), is closely related to the position of the sun (Waterman 1981). The orientation of polarization is perpendicular to the direction of the sun, and maximal polarization is found in regions of the sky located at 90° from it. This close association between the orientation of polarization and the location of the sun was utilized by the Vikings, who used "sun stones", probably calcite crystals, as navigational aids (Konnen 1985). It is also used, for a similar task, by animals such as bees, ants, and possibly birds, and even under partly cloudy skies it permits them to know the location of the sun (Wehner 1976, Fent & Wehner 1985, Phillips & Waldvogel 1988, Able 1989, Phillips & Moore 1992). In addition to polarization induced by scattering, other processes create partial polarization. Dielectrics, such as surfaces covered with wax or water, reflect light that is polarized parallel to their surfaces. Using this property of reflection, several species of aquatic insects can detect water pools while flying (Schwind 1991) and may be able to discriminate between water pools based on their polarization reflection (Schwind 1995). Polarization vision is also involved in target detection (Shashar *et al.* 1995a) and recognition (Moody & Parris 1960, Shashar & Cronin 1996), communication (Shashar *et al.* 1996), and in body orientation (Daumer *et al.* 1963, Hawryshyn & Bolger 1990). Additionally, polarization sensitivity may be used to analyze information associated with small-scale features. Partially linearly polarized light carries several types of information potentially useful to animals. For example, leaves of different plants will reflect light with varying partial polarization (Land 1993). Furthermore, the use of linearly polarized light can to improve object—background discrimination (Lythgoe & Hemming 1967, Shashar *et al.* 1995a).

Among invertebrates polarization sensitivity has been found in insects such as beetles (Jander & Waterman 1960, Schwind 1991), flies (Gribakin & Ukhanov 1993), bugs (Schwind 1991), ants (Fent & Wehner 1985), bees (Wehner *et al.* 1975), butterflies (Bandai *et al.* 1992), and crickets (Labhart 1988); as well as various marine invertebrates (Waterman 1984). Several species of vertebrates, including fish (Hawryshyn 1992), amphibians (Auburn & Taylor 1979), and birds (Able 1989), are also sensitive to polarized light.

However, our own insensitivity to the polarization of light veils the information it carries. To examine the distribution of partially linearly polarized light in nature, and to understand its potential role in animal vision, we examined polarized light fields in a tropical rain forest in Guatopo National Park, Venezuela with a recently developed imaging polarimeter (Cronin *et al.* 1994, Shashar *et al.* 1995b).

METHODS

Partially linearly polarized light was measured using a polarization camera, modified after Wolff & Mancini (1992) and Wolff (1993), enabling measurement of partial polarization and the orientation of polarization throughout an image on a single pixel basis. This sensor is fully described elsewhere (Cronin *et al.* 1994, Shashar *et al.* 1995b). In short, two twisted nematic liquid crystals (TNLCs) are placed in series with a linear polarizing filter fixed at the horizontal (0°) orientation. When TNLCs are relaxed they rotate the plane of polarization of light by a predetermined angle. When voltage is applied, the molecules within the TNLC stretch and no longer rotate the light. By using one TNLC set to produce 90° rotation, and a second for a 45°

rotation, the plane of polarization of the light is rotated by 0°, 45°, and 90°. The polarizing filter only transmits light that is polarized parallel to its own orientation, which was recorded with a Yashica KX-V1 Hi-8 handycam video recorder. Images (single fields) were digitized, in the laboratory, via a frame grabber, to a computer as arrays of 320 (horizontal) × 240 (vertical) pixels, where they were analyzed on a single pixel basis. From consecutive images collected at three orientations, we calculated the partial polarization and orientation of polarization. Spectral sensitivity of the sensor is defined by the sensitivity of the video camera (400–650 nm).

For display, the polarization information in an image was coded into color using the cylindrical HSL (hue, saturation, lightness) map (Hall 1988, Wolff & Mancini 1992). Orientation of polarization, which varies from 0° to 180°, was coded as hue by multiplying the angle by two and therefore using the full 360° hue scale. Partial polarization was coded as saturation, where full saturation represents total polarization, and depolarized light is represented by achromatic gray shades. Lightness remains unaffected, and is proportional to the intensity of the light reflected from the object. This display method enables quick intuitively understandable assessment of polarization information (orientation of polarization and partial polarization) throughout an image. When viewing the false color images, one must bear in mind the limitations of this display method. Orientation differences (coded as hue differences) appear more conspicuous than differences in partial polarization (coded to saturation). Additionally, we perceive several parts of the HSL scale as very similar. For example a change of 10° in the angle of polarization (20° shift in hue on the HSL scale) may convert the displayed color from green to cyan or blue, appearing as a very conspicuous change, or it may all be included in the "green" range, appearing as a less significant shift between different "greens" (see Fig. 1 as an example). Nevertheless, a full numerical analysis is also available, and this transformation is a powerful tool for presenting all three characteristics of partially linearly polarized light. We must emphasize that we do not imply that any animal actually perceives polarization information in this manner.

The study was conducted at the tropical rain forest of Guatopo National Park, Venezuela (10°03′ N, 66°28′ W) at 300–400 elev. This is a "Very Humid Premontane" life zone (following the Holdridge life zone system; Ewel *et al.* 1976). Average monthly temperature ranges from 27.7–17.9°C (O'Connell 1981). Annual rain fall is 1.5–2 m, with a rainy season (May to December) when monthly rain can reach 350 mm, and a drier season (January to April) with no less than 50 mm rainfall per month (O'Connell, 1981). However the forest is evergreen without seasonally deciduous trees.

Measurements were performed, over 21 days and more than 25 hours of recording, in a variety of locations within the rain forest, in different weather conditions, throughout the day from sunrise to sunset. We examined large scale patterns, such as the sky, as well as at distinct objects such as single leaves or individual animals. With a sampling rate of 5–10 Hz and over 75,000 measurement points per sample (per image), statistical analysis between samples is not useful and is driven by the characteristics of the video recording (length, acceptance angle, magnification, overlap between frames, *etc.*). Therefore we present only patterns which were consistent throughout most of the day and at several distinct sites. In all cases, the polarization image was compared to the RGB full color image to evaluate the specific information it might contain.

RESULTS

Distinct patterns of the characteristics of polarization of the light field were identified in measurements throughout the rain forest. These patterns can be examined at several scales.

Overall characteristics of polarized light fields.—As expected, strong polarization in the sky was measured in regions located at 90° from the sun (Fig. 1). The polarization of the sky can be seen even from beneath the canopy (Fig. 1) and can be used by animals living at lower parts of the forest, as long as they have a clear view of a large portion of the sky. However, sky polarization was reduced and even totally diminished under heavy clouds or fog (Figs. 1, 3-top).

Within the rain forest the dense foliage limits the penetration of light and in many cases direct light arrives from only a small region of the sky. When the light scattered from this region is strongly polarized, it creates a light source to the forest that is linearly polarized (Fig. 2). This is a very unusual circumstance in nature, in which the light source itself is polarized. Under these conditions, light reflected from most objects will be polarized as well, and at a similar orientation to that of the light source (Fig. 2). Any object, such as insect cuticle, reflecting light polarized at

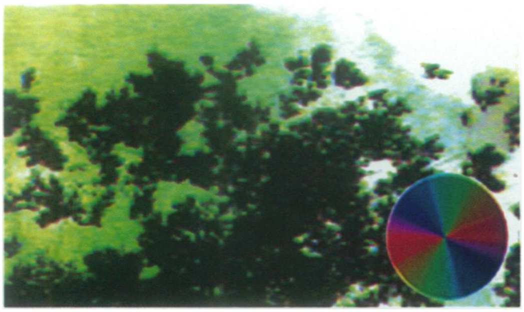

FIGURE 1. A false color polarization image of the sky, as seen from underneath a tree canopy (at 0830 looking toward SW). Polarized light reflected from the sky can be seen through the canopy of a tree. Clouds however, depolarize the incoming light. In this figure, the light polarization is coded to color on the HSL scale. The insert shows the coding map of angle of polarization as hue (by multiplying the angle of polarization by 2, where for example, a polarization angle of 135° is coded as a 270° hue which appears as blue. Partial polarization is coded as saturation on a 0–1 scale and lightness remains that of the reflected light (see text for details). Therefore, the "green" colors of the sky represent angles of polarization of 50–62°, depending on the location in the sky.

FIGURE 2. False color polarization image of a *canopy hole shade* in the forest. The light arriving from the sky is polarized at 20. 0 ± 7. 6°C (x ± SD, N = 576 pixels; horizontal is defined as 0°) while that reflected from objects throughout the image is polarized at 20.2 ± 10. 3°C (x ± SD, N = 5676 pixels; shaded parts of the image were excluded) and are therefore coded to red-orange. This is an unusual situation where the light source itself is partially polarized, and therefore most objects appear polarized at a similar orientation.

a different orientation, due to its spatial orientation or material, may become very conspicuous in such conditions.

Under depolarized illumination, or when the light is arriving from several regions of the sky, the polarization of reflected light is less homogeneous. Light reflected from surfaces, especially moist ones, tends to be polarized parallel to the surface. From a distance of over 25 m, the pattern of polarization is determined by the particular regions within the forest from which the light arrives (Fig. 3, top). Light reflected from the vertical sides of trees and climbing plants is generally vertically polarized, while the polarization of light reflected from leaves in the canopy has a predominantly horizontal orientation. Furthermore, each leaf has its own specific reflection pattern (Fig. 3, middle and bottom). The combination of these effects creates a complex pattern of polarization, even in regions that appear dominantly green using wavelength (color) spectrum.

In the shadows of the forest, the sky is mostly obscured, and objects are illuminated through secondary and higher order reflections. Although one may expect polarization signals to diminish under such conditions, our measurements show that even in deeply shaded regions, light reflected from leaves is partially polarized parallel to their surfaces.

Reflections from single objects.—Entire leaves, or different parts of a single leaf, will reflect differentially polarized light according to their spatial positions and structure (Fig. 3, bottom). Moisture on leaves or their waxy cuticle can influence the partial polarization. However, these factors do not affect the orientation of polarization, which depends on the surface orientation. Therefore, the orientation of polarization can provide information about the spatial position of the surface.

Beside indicating the spatial orientation of objects, polarized light may reveal the presence of chromatically well camouflaged objects. Fig. 4 illustrates a camouflaged moth caterpillar (*Megalopyge* sp.) which is very difficult to distinguish from the orange leaf on which it is sitting, except possibly for shaded areas on both its sides. Despite its chromatically matched camouflage, the caterpillar becomes conspicuous when the pattern of polarization is analyzed. The numerous hairs of the *Megalopyge* reflect light at various orientations, evident when the variance between the polarization angle at each point and that of its neighbors is analyzed. High variation is apparent all over the caterpillar's body, but is rare in the homogenous reflection from the leaf on both sides of the animal.

Analysis of partial polarization can be used for breaking camouflage as well. The toad *Bufo typhonius* in Figure 5 is chromatically camouflaged on the background of foliage from the forest floor. With the exception of the right side of the toad, the orientation of polarization of light reflected

FIGURE 3. False color polarization (left) and full color (right) images of trees on different scales. The insert demonstrates the coding of angle of polarization into hue; percent polarization (partial polarization) is coded into saturation, as in Figure 1. From a distance of over 25 m (top) the pattern of polarization basically follows the contour of the trees. On closer (7–10 m) examination (middle) every leaf has its own polarization characteristics, depending on its orientation and texture. When a single *Gurania spinulosa* leaf is viewed (bottom), the polarization orientation of light reflected from its surface is related to the orientation of the surface at each point. The numbers in the left image indicate the orientation of polarization of light reflected from specific points.

from the leaf and the toad is within the 130°-180° range, and therefore could be used to discriminate only one side of the animal. However, the leaves reflect light that is about 10–20 percent polarized, while light reflected from the moist skin of the toad is over 40 percent polarized. Therefore variations in partial polarization can indicate differences in surface makeup.

DISCUSSION

The light environment in a rain forest forms a very diverse set of patterns (Chazdon & Fetcher 1984a, Chazdon *et al.* 1996, Pearcy 1990, Smith *et al.* 1992). Regions of full and intense sunlight lie adjacent to areas of relative darkness. Some parts of the forest are always shaded and are illuminated primarily by light reflected or scattered from other objects, other locations receive short bursts of solar illumination known as sunflecks. Some areas obtain direct sunlight only during short periods of the day and only from a narrow region of the sky, while others are illuminated through most of the day. Light conditions may vary rapidly as clouds cover the sky or as a tree shadow moves with the wind. Direct field measurements of polarized light reveal that the polarization distribution is complex as well, and that it presents a pattern very different from that seen through intensity and color vision.

What information can be provided by the polarization of light? The orientation of polarization is closely related to the orientation of the surface of the

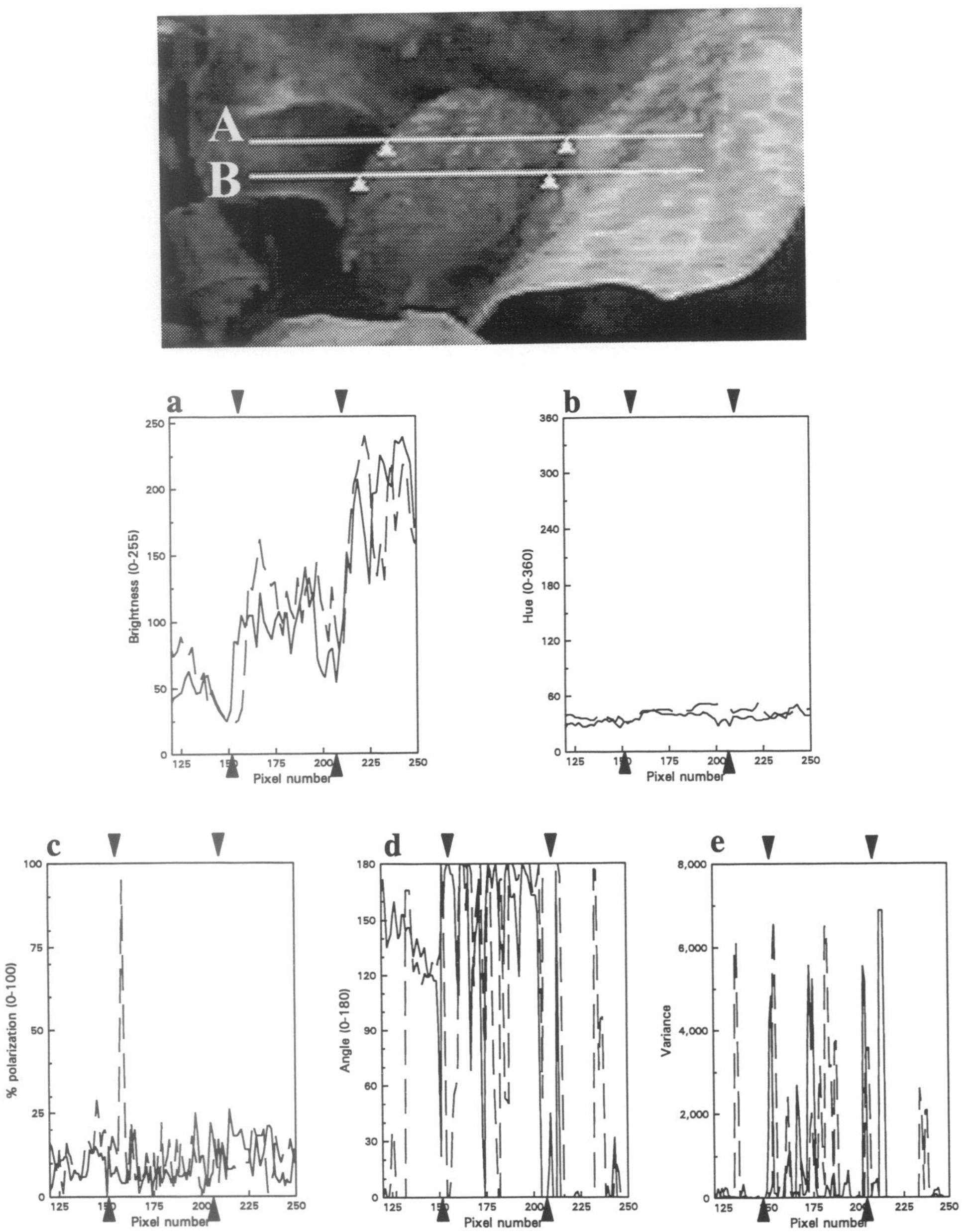

FIGURE 4. A *Megalopyge* sp. caterpillar on a leaf, viewed under natural light conditions. Characteristics of the reflected light (a-brightness, a-hue, c-percent of polarization and d-polarization angle) along two transects are graphically presented. Arrows indicate the edges of the animal; the dashed line, and the arrows at the top of each insert correspond with transect A; the continuing line and arrows at the bottom of each transect correspond with transect B. Brightness (lightness) is displayed on a 0 to 255 scale, and hue is presented on the 0–360 HSL scale. The abscissa (pixel number) is the horizontal location of the pixel measured in the 320 (H) × 240 (V) image, where its origin lies on image lower left corner. Neither hue (b) nor partial polarization (c) show an indicative difference between the caterpillar and the leaf. Similarly, the only indication on the brightness scale (a) are the shadows at the edge on the animal's body. However, due to the complex surface, the light from the caterpillar is reflected at various polarization angles, while the reflected from the leaf is polarized at a constant, mainly horizontal, orientation (d). This phenomenon is more evident (e) when the variance (σ^2) of the angle of polarization in the neighborhood of each pixel, 5 pixels in each direction along the horizontal transect ($N = 11$) is presented.

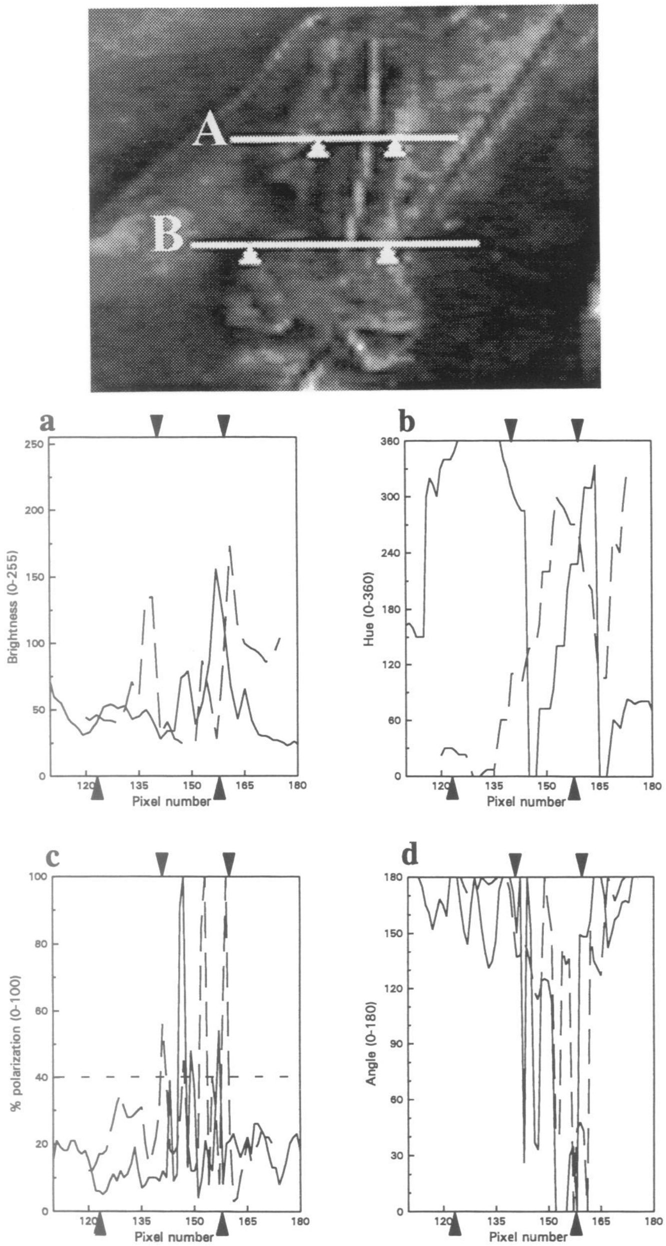

FIGURE 5. A *Bufo typhonius* on a leaf. Characteristics of reflected light are presented as in Figure 4. Neither brightness (a), hue (b) nor orientation of polarization (d) show clear differences between the toad and its background. However, the partial polarization (c) of the light reflected from the toad is higher, and more variable, than that reflected from the leaf. As an example, only the toad reflects light that is more than 40 percent polarized (dotted line). Kindly identified by Dr. R. McDirmid. The genus *Bufo* has not yet been fully studied in Venezuela, and it is conceivable that under the "*typhonius*" name are actually several distinct species.

reflecting object (Kliger *et al.* 1990). Therefore, knowing the orientation of polarization determines constraints on an object's orientation (Wolff & Boult 1991), and two independent measurements can provide its exact spatial orientation. The orientation of surfaces is important information for flying animals, both on a large scale, as the orientation of trees and tree tops, and on a small scale such as the positioning of a single leaf. The latter is especially important during landing on an object.

Borders of objects, and borders between objects, can be emphasized by polarized light. Though neighboring leaves may have similar colors, and may reflect light of similar brightness, the light reflected from their surfaces can be polarized at distinct orientations, creating a clear contrast between them. Polarization-based border enhancement could improve object detection. This may provide greater detection range, or a better discrimination between objects under contrast limiting conditions. Such enhancement is of great potential advantage for predators, prey, or conspecifics, and may be useful in intraspecific communication.

Material classification is another possible function of polarization vision (Wolff 1990). Land (1993) showed that different leaves will reflect light with different partial polarization, depending on the nature of their coating. Similarly, the moist skin of a toad reflects light that is more strongly polarized than that reflected from the surrounding leaves (Fig. 5). Local variations in the orientation of polarization provide additional cues that can be used for discriminating between hairy or fuzzy material and smooth surfaces.

Enhancement of borders, or other differences between objects can be utilized for breaking biological camouflage. Animals are able to discriminate between targets using it (Moody & Parris 1960, Rowell & Wells 1961, Shashar & Cronin 1996) and may be using polarization vision for communication (Shashar *et al.* 1996). However, behavioral experiments are still required to examine the applicability of this visual channel for animals living within the rain forest.

The light environment in rainforests is well studied (*e.g.*, Chazdon & Fetcher 1984b, Pearcy 1990, Smith *et al.* 1992; see reviews by Chazdon & Fetcher 1984a, Chazdon *et al.* 1996). We here follow the description of Endler (1993), as his study focused on questions particularly related to vision. Based on intensity and hue information, Endler (1993) categorized five major light environments in forests. These environments were named *forest shade, woodland shade, large* and *small gaps, open/cloudy* and *early/late*. In Table 1 we describe how these environments vary in their polarization light field. The *woodland shade, large gaps*, and *open* regions (for exact description see Endler 1993) have much in common, as polarized light in the sky is visible through much of the day. This is due to the fact that in the sky, the distribution of polarization is based on scattering and not on direct sunlight. In these forest regions polarization sensitivity could be utilized for navigation as well as for pattern and texture recognition. *Small gaps* are regions that receive direct sunlight. As sunlight itself is depolarized, the light field is not polarized, and polarization arises only from reflection from objects such as leaves and animals. Similar to the *small gaps* are the regions we call *canopy hole shade,* where light arrives from only a small region of the sky, but not directly from the sun (according to Endler's classification they are part of the *woodland shade* category). In this category celestial scattering can create a polarized light source. Polarization could be used for navigation in these areas only with difficulty but could be more useful for pattern and texture recognition. Obviously, an area can shift between the *small gaps* and the *canopy hole shade* light environments according to the movement of the sun in the sky. The last category is the *forest shade.* These are areas that do not receive direct sunlight and in which all light has been reflected from or transmitted through leaves. In these areas, as in the *small gaps,* the polarization pattern can be used only for analyses of surface orientation and texture.

Two overcast states, which influence the polarization distribution, have been identified. These states are associated with the position of the sun in the sky and with the existence of clouds and fog. The position of the sun dictates the polarization pattern of the light coming from the sky and causes it to change throughout the day. Clouds and fog scatter light and therefore depolarize incoming light. These states will affect all the light environments, but will have relatively little effect on the *small gaps* and the *forest shade,* since these light fields are always depolarized (Table 1).

In this paper we described several aspects of the distribution of partially linearly polarized light in a tropical rain forest and considered possible applications of polarization sensitivity. We showed that polarization vision can be used to perform tasks for which brightness and spectral sensitivity alone are not sufficient. Currently, lack of knowledge of the sensitivity to polarized light of the inhabitants of the rain forest limits our understanding of its biological significance. Nevertheless, many rain forest animals are closely related to species in which polarization sensitivity has been identified. Further study of the visual systems of these animals is required for better understanding of the complex visual environment existing in tropical rain forests.

TABLE 1. *Characteristics of the light field, and the effects of clouds (indicated in italics), at several light environments in tropical rain forests.*

Light environment	Main illumination source	Light characteristics		
		Intensity[1]	Chromaticity[2]	Polarization[3]
Open areas (Endlers Sunny/cloudy)	Direct sunlight	100%	Dominated by the sun's spectrum.	Dominated by the celestial polarization pattern.
Clouds effect		*no effect*	*no effect*	*Light field* is *depolarized.*
Large gaps	Direct sunlight	94%	Dominated by the sun's spectrum.	Dominated by the celestial polarization pattern.
Clouds effect		*no effect*	*no effect*	*Light field is depolarized.*
Small gaps	Direct sunlight	22%	Long wavelength (red) dominated.	Light field is depolarized.
Clouds effect		*intensity decreases*	*Spectra shift to those of the large gaps.*	*no effect*
Woodland shade	Blue sky	2.5%	Short wavelength (blue) dominated.	Dominated by the celestial polarization pattern.
Clouds effect		*intensity decreases*	*Spectra shift to those of the large gaps.*	*little effect*
Canopy hole shade (part of Endlers Woodland shade)	Blue sky	2.5%	Short wavelength (blue) dominated.	Light field is polarized at the orientation of the light source.
Clouds effect		*intensity decreases*	*Spectra shift to those of the large gaps.*	*Light field is polarized*
Forest shade	Vegetation reflection	1.3%	Dominated by green leaf reflectance.	Light field is depolarized.
Clouds effect		*intensity decreases*	*Spectra shift to those of the large gaps.*	*no effect*

[1] Recalculated from total intensity (400–700 nm) averages between 0900 and 1500 in Endler (1993). Open spaces (avg. 1164 μmole/m^2/sec) referred to as 100%. See also Chazdon & Fetcher (1984).
[2] After Endler (1993).
[3] Current study.

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