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Natural History Note

Differential Response to Circularly Polarized Light by the Jewel Scarab Beetle *Chrysina gloriosa*

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ABSTRACT: Circularly polarized light is rare in the terrestrial environment, and cuticular reflections from scarab beetles are one of the few natural sources. *Chrysina gloriosa* LeConte 1854, a scarab beetle found in montane juniper forests of the extreme southwestern United States and northern Mexico, are camouflaged in juniper foliage; however, when viewed with right circularly polarizing filters, the beetles exhibit a stark black contrast. Given the polarization-specific changes in the appearance of *C. gloriosa*, we hypothesized that *C. gloriosa* can detect circularly polarized light. We tested for phototactic response and differential flight orientation of *C. gloriosa* toward different light stimuli. *Chrysina gloriosa* exhibited (a) positive phototaxis, (b) differential flight orientation between linear and circularly polarized light stimuli of equal intensities, and (c) discrimination between circularly polarized and unpolarized lights of different intensities consistent with a model of circular polarization sensitivity based on a quarter-wave plate. These results demonstrate that *C. gloriosa* beetles respond differentially to circularly polarized light. In contrast, *Chrysina woodi* Horn 1885, a close relative with reduced circularly polarized reflection, exhibited no phototactic discrimination between linear and circularly polarized light. Circularly polarized sensitivity may allow *C. gloriosa* to perceive and communicate with conspecifics that remain cryptic to predators, reducing indirect costs of communication.

Keywords: circularly polarized light, scarab beetles, polarization sensitivity, phototaxis.

Introduction

The immense diversity of beetles inspired J. B. S. Haldane's famous musing of a possible Creator having "an inordinate fondness of beetles" (Hutchinson 1959, p. 146). Yet the morphological diversity in beetles goes well beyond what we can see with the unaided eye. Jewel scarabs, and related beetles, have fascinated both naturalists and physicists in possessing a unique form of reflection in their iridescent

colors, circularly polarized light (Michelson 1911; Caveney 1971; Seago et al. 2009). Circularly polarized light is a relatively rare form of polarized light (Hannemann and Raschke 1974) that differs from linearly and elliptically polarized light in the propagation of the electric field or e-vector.

Linearly polarized (LP) light has an e-vector that oscillates uniformly in one plane; it is common in skylight, underwater, and terrestrial environments; and it is produced by scattering and reflection with dielectric particles and surfaces. Circular and elliptically polarized light have e-vector oscillations that rotate as the wave travels. Circularly polarized (CP) light consists of two perpendicular waves of equal amplitude that are phase shifted by 90°, resulting in e-vectors rotating in either a clockwise (called right circularly polarized [RCP]) or counterclockwise (called left circularly polarized [LCP]) direction when looking into the direction of propagation of the beam (Hecht 1998). Elliptically polarized light is a coherent combination of linearly and circularly polarized light consisting of two perpendicular waves of unequal amplitude that are out of phase by some constant degree and is commonly found underwater (Kattawar and Adams 1989).

The rarity of circularly polarized light in nature presents itself as an opportunity for unique signal evolution—a signal that can contrast against linearly polarized backgrounds while being cryptic in color. In theory, *Chrysina gloriosa* can chromatically blend into the background to hide from viewers lacking polarization-detecting abilities while simultaneously exhibiting strong polarization contrast for viewers with circularly polarized visual sensitivity (see fig. 1). Another possible biological advantage of circularly polarized light is that there is no preferential angle from which to detect the polarization, as is the case with the linearly polarized light off of water surfaces (Horváth et al. 2008). The directionality of linearly polarized light is useful for orientation and navigation (see, e.g., Baylor and Smith 1953; Waterman and Forward 1972; Waterman

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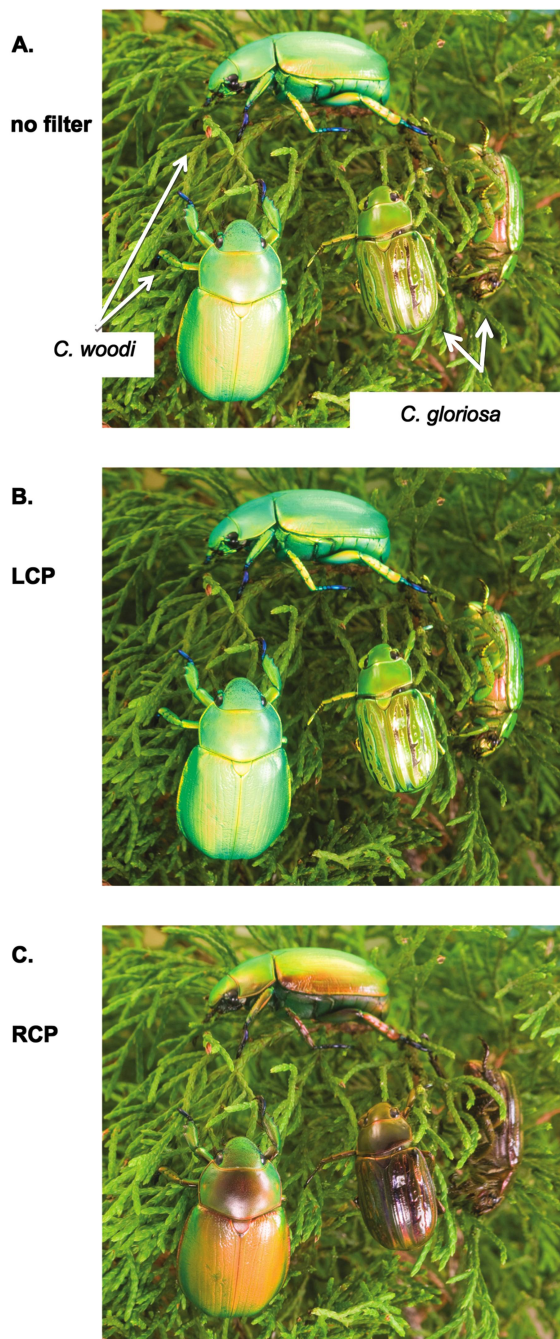


Figure 1: Photographs of *Chrysina gloriosa* (smaller) and *Chrysina woodi* (larger) on juniper branches, with (A) no filter and (B) left circularly polarized and (C) right circularly polarized filters. Photographs by John C. Abbott.

1981, 2006; Shashar et al. 2005) but may represent a challenge for conspecific communication because the orientation of both the sender and the receiver may have to be coordinated to achieve successful communication. This

problem is similar to that associated with iridescent signaling, which depends on the direction of view (Rutowski et al. 2007), although iridescent and polarized communication have been reported in some butterflies (Sweeney et al. 2003). Animals using CP light to communicate can send and receive signals regardless of their respective orientations.

Circularly polarized reflection appears limited to only a few groups of organisms, including some scarab beetles and marine stomatopods. Some marine stomatopods exhibit sexually dimorphic circularly polarizing reflective patches on their tails (Chiou et al. 2008). The unique optical properties of scarab circularly polarized reflections are found in the helical microfibril layers in the exocuticle that act as specialized multilayer reflectors (Chapman 1998). In *Chrysina* sp. the microfibril layers are strongly birefringent as a result of uric acid (a strongly birefringent crystal) in their microfibril layers (Caveney 1971). If the helicity of the microfibril layers is comparable to the wavelength of the incoming light, the light will reflect as circularly polarized light (Jewell et al. 2007).

While most of the circularly polarized reflections of scarab beetles are not very intense, the majority of beetles from the genus *Chrysina* show dramatic and vivid circularly polarized reflection in a variety of colors, including broad-band reflections (Goldstein 2006; Hegedüs et al. 2006a). For example, the entire carapace of *C. gloriosa* LeConte 1854 is highly LCP. The carapace of *C. gloriosa* is green and gold when observed without a filter (fig. 1A) or with LCP (fig. 1B) or LP (photo not shown) filters; however, it changes to black when viewed through an RCP filter (fig. 1C). These beetles are mostly crepuscular and nocturnal but are reported to forage in juniper trees during the day, where they are extremely well camouflaged (Young 1957). Another member of the genus is *Chrysina woodi* Horn 1885, which is also left circularly polarized (fig. 1), to a lesser degree than *C. gloriosa*, and blends in very well with its host plant, the walnut. We hypothesized that these beetles may have circular polarization sensitivity or vision to aid in the detection of conspecifics while allowing them to remain cryptic to predators. In this study, we examine whether *C. gloriosa* beetles are capable of distinguishing circularly polarized light from linearly polarized and unpolarized (UP) light stimuli as a first step in determining sensitivity to circular polarization in this system. We define polarized sensitivity as the ability to distinguish between two different polarized stimuli of the same intensity as opposed to polarized vision where the two stimuli are perceived as different physiological states (akin to different hues in color vision).

To date, the marine stomatopod (*Odontodactylus* sp.) is the only organism with known visual capacity to detect circularly polarized light determined through behavioral

discrimination between right and left circularly polarized stimuli. Optical anatomy and electrophysiology were used to determine the visual sensitivity and mechanism behind circularly polarized detection (Chiou et al. 2008; Kleinlogel and White 2008). These stomatopods most likely use CP light sensitivity for conspecific communication and also perhaps to enhance contrast in turbid media (Chiou et al. 2008).

To determine whether *C. gloriosa* are capable of detecting circularly polarized light, we use a well-known behavioral feature of many beetles: positive phototaxis, the tendency to move toward a bright light source (Longcore and Longcore 2006). Phototaxis has been used to examine sensitivity to linear polarization in several studies involving many different insects (Danthanarayana and Dashper 1986; Horváth and Varjú 2004). We test for the presence of a phototactic response with unpolarized stimuli in *C. gloriosa* and then exploit this response to determine whether these beetles are sensitive to light stimuli with different polarization characteristics. Measuring a nonrandom phototactic response between unpolarized light and circularly polarized light at the same intensity will, by definition, show that *C. gloriosa* has circularly polarized light sensitivity. We then take advantage of the intensity-modifying effects of polarization-sensitive cells to provide stronger support for circularly polarized sensitivity by testing for a reversal in phototactic response (choosing the dimmer unpolarized stimulus over a brighter circularly polarized stimulus).

Material and Methods

In the summers of 2007 and 2008, 54 male and 2 female *Chrysina gloriosa* and 14 male *Chrysina woodi* were collected at the Nature Conservancy in the Texas Davis Mountains. Males were used mainly because of the difficulty of finding females. We performed five experiments with each beetle in the experimental chamber depicted in figure 2. The experimental chamber consisted of a $50.8 \times 50.8 \times 33.0$ -cm box with 3.8×3.8 -cm square slits centrally located on each of three sides for stimuli presentation and the fourth side used for flight observations. Stimuli consisted of optical filters, each illuminated with a 250-W halogen light bulb at a 30-cm distance. The mirror reflection surface associated with the halogen lamp was metal and did not significantly reflect polarized light due to Fresnel reflections. For phototaxis experiments, stimuli consisted of a bright (UP light with two 0.3 neutral density [ND] filters, GamColor 1515) and a dark (UP light with three 0.3 ND filters) stimulus. Polarization experiments included comparisons between an LP stimulus consisting of a vertically oriented linearly polarizing filter (PF006, Alight, San Antonio, TX; transmission $\sim 38\%$ or

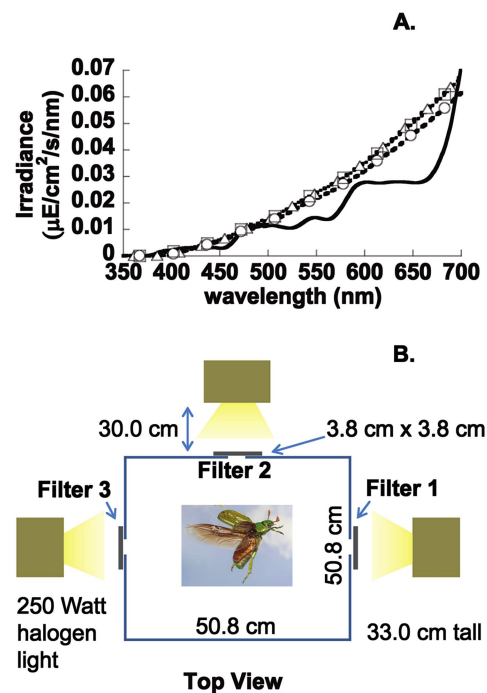


Figure 2: A, Spectral irradiance spectra ($\mu\text{Einsteins}/\text{cm}^2/\text{s}/\text{nm}$) of the different experimental stimuli: linearly polarized (squares), left circularly polarized (triangles), right circularly polarized (circles), and unpolarized (solid line). B, The experimental design consisted of a choice chamber with up to three slots for filter presentation that was backlit with halogen lights.

ND = 0.42 of UP light); LCP and RCP stimuli, each composed of an LP filter followed by a quarter-wave plate with optimal wavelength at 560 nm and high transmission (WF-OG4, Alight, San Antonio, TX) in opposing orientations; and a UP stimulus (UP light with two 0.3 ND filters). We used a vertically oriented LP filter because the polarized field that these beetles would be exposed to would be from leaves, and vertical polarized light will be a dominating orientation of polarized light in this environment.

We used a matte black box to reduce experimental noise associated with phototaxis. A potential problem with using black backgrounds for polarization experiments is the Umow effect, where black backgrounds reflect higher percentages of polarized light than white backgrounds, increasing the chance of spurious polarized signals (Horváth and Varjú 2004). These effects are not likely to significantly affect our results because of our box configuration. Reflected light off of the sides of the box will be at angles that will have minimal polarized Fresnel reflection relative to the test subject. Also, the light from the stimulus will be several orders of magnitude brighter than light reflected off the sides of the box.

Spectral irradiance, $I(\lambda)$, measures of the various stimuli were collected with a StellarNet (Tampa, FL) EPP2000C spectrometer and cosine collector stationed in the same position as the beetle stand (fig. 2A). The polarized stimuli showed similar intensities ($\log I(\lambda)$, integrating over 300–700 nm): LP = 0.913, LCP = 0.914, RCP = 0.872, with an inadvertent flux difference of 5% between the two CP light stimuli. All polarized stimuli were more intense than the UP stimulus (UP = 0.744, representing a 15%–19% difference in intensity).

Each beetle in the chamber was placed on a 2.5-cm stand in the center of the chamber, initially facing the center stimulus position (fig. 2B). All the beetles used were in the same phototactic state. They were flown between the hours of 22:00 and 2:00. To account for position bias, each beetle was tested on two consecutive nights, with the stimuli (filter) position altered between trials, with up to four flights recorded per trial. The stimuli filters were rotated cyclically between trials, such that each stimulus (LP vs. RCP vs. LCP or UP vs. LCP vs. RCP) was positioned in each of the three experimental slots (left, right, center) in approximately one-third of all trials. For double-choice experiments (bright vs. dark phototaxis; LP vs. LCP), the center slot remained empty and stimuli were changed from right and left sides between trials. To control for different number of total flights performed by different beetles, only the initial flight direction for each trial was used in statistical analyses (Kruskal-Wallis [K-W] and Wilcoxon signed pairs tests).

The “bright versus dark phototaxis” experiment was used to establish positive phototaxis as a basis for the rest of the experiments. The “UP versus LCP versus RCP” experiment was used for determining sensitivity to circular polarization. We used LP stimuli to establish the relative relationship between CP and LP light in this system and to provide contrasting results.

Results

Chrysina gloriosa beetles exhibited significant nonrandom orientation toward specific stimuli in all experiments. In the phototactic experiments, *C. gloriosa* beetles showed no position bias (left vs. right flights, $Z = 0.76$, $n = 28$ trials [14 beetles], $P = .45$) while exhibiting a highly significant differential response toward the brighter unpolarized stimulus ($Z = 3.02$, $P = .002$; fig. 3A), indicating a positive phototaxis response.

In the first polarization experiment (LP vs. LCP vs. RCP), we found no position bias (K-W = 0.61, $n = 32$, $P = .74$) yet highly significant differential orientation among stimuli polarization (K-W = 18.96, $P < .0001$; fig. 3B). Post hoc pairwise analyses show a graded response between the LP versus the CP light stimuli (LP vs. LCP,

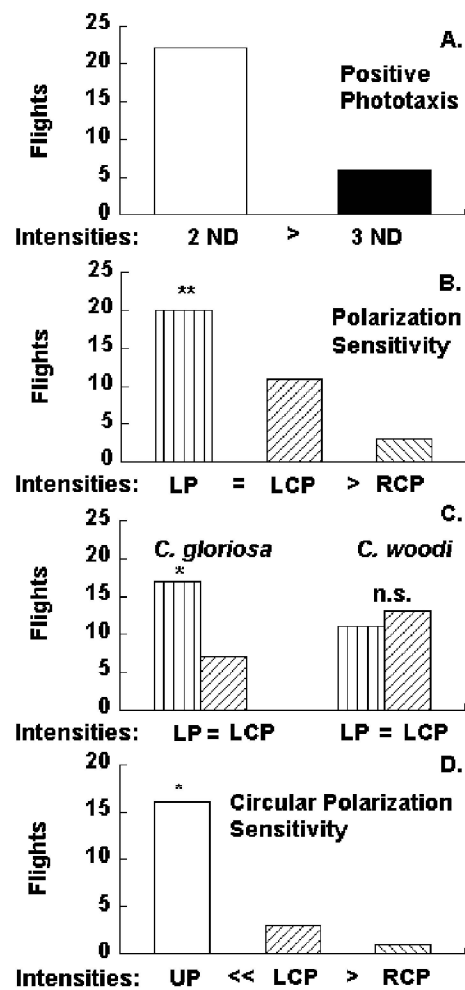


Figure 3: Phototaxis and polarization experiment results reporting the total number of the first flights toward the stimulus per trial. A, *Chrysina gloriosa* flights toward bright (white; unpolarized light with two neutral density filters) and dark (black; unpolarized light with three neutral density filters) stimuli and (B) toward linearly polarized light (LP, left) versus left circularly polarized light (LCP, middle) and right circularly polarized light (RCP, right) of similar intensities. C, Species comparison of LP versus LCP. D, *Chrysina gloriosa* flights toward the darker UP (unpolarized light with two neutral density filters; white) versus the brighter LCP and RCP stimuli.

$Z = 1.6$, $P = .11$; LCP vs. RCP, $Z = 2.14$, $P = .03$), which was consistent with the differences in stimuli intensities. To remove intensity differences, the experiment was repeated with a different set of 12 *C. gloriosa* beetles in a double choice between LP and LCP of equal intensities. This experiment confirmed the differential response between LP and CP light stimuli ($Z = 2.04$, $n = 24$ trials, $P = .04$; fig. 3C) with no position bias ($Z = 0.41$, $P = .68$). Conducting the same experiment with *Chrysina woodi* beetles, we found no discrimination in flight ori-

entation between LP and CP light stimuli ($Z = 0.41$, $n = 24$ [12 beetles], $P = .68$; fig. 3C), yet they did exhibit a position bias (right > left flights, $Z = 2.04$, $P = .04$).

In our test of unpolarized versus circular polarization discrimination (UP vs. RCP vs. LCP), where UP was 15%–19% lower in intensity, we found no significant position bias ($n = 20$ trials, K-W = 5.45, $P = .07$) but a highly significant stimuli bias (K-W = 29.35, $P < .0001$; fig. 3D), with *C. gloriosa* beetles favoring the less intense UP stimuli.

Discussion

Chrysina gloriosa exhibited strong positive phototaxis, orienting their flights toward brighter over dimmer unpolarized stimuli (fig. 3A). Moreover, *C. gloriosa* exhibited significant differences in flight orientation depending on the polarization characteristics of the stimuli. The first two polarization experiments (fig. 3B, 3C) demonstrated that *C. gloriosa* can distinguish between linearly and circularly polarized light, indicating that *C. gloriosa* beetles have linear polarization sensitivity and/or circular polarization sensitivity. Our final experiment (fig. 3D) demonstrated that *C. gloriosa* can differentiate between circularly polarized and unpolarized light. These results support the hypothesis that *C. gloriosa* has circularly polarized light sensitivity, which is a first step in determining circular polarization vision. The fact that *C. gloriosa* have dramatic, yet cryptic, circularly polarized reflections from their carapace strongly supports the hypothesis that they have ecologically important circular polarization vision.

Molecular Basis for Polarization Sensitivity

Insect polarization sensitivity is the result of organelles in the ommatidia that contain rhodopsin molecules in aligned patches of microvilli (Chapman 1998). Rhodopsin molecules preferentially absorb light depending on their alignment with the e-vector of the light wave, with absorption being greatest when the e-vector is parallel to the rhodopsin molecule (Horváth and Varjú 2004). The arrangement of microvilli within the rhabdom can significantly affect sensitivity to polarized light (Horváth and Varjú 2004). Light with a polarization angle that is parallel to the microvilli is perceived as much more intense compared to light with a polarization angle perpendicular to the microvilli.

Lepidopterans that are sensitive to linearly polarized light exhibit phototaxis toward unpolarized light stimuli more than three times as frequently as they do toward horizontally or vertically polarized light stimuli of equal intensities under comparable field conditions (Danthanarayana and Dashper 1986). These observations suggest that polarization sensitivity can result in lower perceived

intensity of polarized light relative to unpolarized light. This idea is supported by physiological measurements showing dark adaptation responses to polarized light being weaker than those toward unpolarized light in the moth *Laspeyresia pomonella* (L.) (Danthanarayana and Dashper 1986). Nonetheless, there are accounts of some insects exhibiting a stronger response toward linearly polarized stimuli over unpolarized light at similar intensities. Hence, the phototactic response in relation to polarized light is likely unique for each insect species, as species vary in the orientation and alignment of the microvilli as well as the relative number of dedicated polarization-sensitive cells.

Sensitivity to Circularly Polarized Light in *C. gloriosa*

Linear polarization detectors, such as the microvilli/rhodopsin detectors in insect eyes, cannot physically distinguish circularly polarized light from unpolarized light at the same intensity (Hecht 1998). Without additional modifications to the insect eye, circularly polarized light would be absorbed by the same fraction of rhodopsin molecules as unpolarized light, leading to the same degree of receptor activation and thus the same perceived intensity. In this study, *C. gloriosa*, a positively phototactic beetle, responded more strongly to linear polarized and unpolarized light of equal or lesser intensities than to circularly polarized light (fig. 3). Such a differential response suggests that *C. gloriosa* have unique optical features that specifically reduce the perceived intensity of circularly polarized light relative to unpolarized or linearly polarized light.

A linear polarization-detecting rhabdom can be modified to detect circular polarization. Circularly polarized light can be converted into linearly polarized light and vice versa when propagating through a properly aligned birefringent medium called a quarter-wave plate. Thus, capping the rhabdom with a quarter-wave plate effectively changes the linear-polarization-detecting faculty into a circular-polarization-detecting faculty. A portion of the rhabdoms of stomatopods (*Odontodactylus* sp.) are capped with a quarter-wave plate, resulting in circularly polarized light detection (Chiou et al. 2008; Kleinlogel and White 2008).

Our experiments indicate that *C. gloriosa* shows a distinct ability to differentiate unpolarized light from circularly polarized light with phototaxis; under conditions of lower unpolarized intensities, we have initial evidence that *C. gloriosa* exhibits circularly polarized light sensitivity, which is consistent with a quarter-wave plate capped photoreceptor mechanism of detection. The differential response toward the unpolarized light at a lower overall intensity suggests that the circularly polarized sensitivity in *C. gloriosa* reduces intensity perception; however, further investigation of the specific visual mechanism in *C. gloriosa* is required.

Ecological Implications for Circular Polarization Vision

Since the discovery over 60 years ago (Verkhovskaya 1940; von Frisch 1949; Waterman 1981) of orientation to linearly polarized light by some animals, a number of animals have been shown to use linear polarization for navigation, foraging, and communication (Shashar et al. 1996; Marshall et al. 1999; Hegedüs et al. 2006b; Lerner et al. 2008). The rare occurrence of circularly polarized light in the natural environment suggests that circularly polarized light may be a means for some animals to communicate without detection by heterospecifics. Future studies examining the behavioral responses of *C. gloriosa* and predators toward beetles with manipulated polarized reflection will determine whether it serves a role in communication or camouflage.

Interestingly, the congener, *Chrysina woodi*, exhibited no differentiation between linearly polarized and circularly polarized light (fig. 3C) while also exhibiting less differential circularly polarized reflection than *C. gloriosa* (fig. 1). The acquisition of both circularly polarized light reflection and sensitivity in *C. gloriosa* may have evolved separately or jointly. In other insects, wing coloration pigments (ommochromes) also serve as screening pigments in the eye (Kronforst et al. 2006). If the birefringent material responsible for the circularly polarized light reflection on the beetles' carapaces also serves as a wave plate mechanism in the ommatidia, then signal production and reception may be linked. As support for this idea, measurements in other beetles have revealed that their corneal lenses are birefringent (Meyer-Rochow 1973). The coevolution of circularly polarized coloration and sensory processing in *C. gloriosa*, whether driven by a joint mechanism or not, results in this beetle having an unusual means of seeing and being seen in this world.

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Jewel scarab in flight (*top*) and view of jewel scarab habitat at the Nature Conservancy Davis Mountains Preserve in west Texas (*bottom*). Photographs by John C. Abbott/Abbott Nature Photography.