HIDING FROM THE GHOST OF HERBIVORY PAST: EVIDENCE FOR CRYPSIS IN AN INSULAR TREE SPECIES

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The color of many animals matches that of their preferred habitats, making them difficult for predators to locate. However, quantitative examples of crypsis in plants are comparatively rare. We conducted morphometric and spectrographic analyses of a heteroblastic tree species that is endemic to New Zealand (*Elaeocarpus hookerianus* Raoul) to test whether it is cryptic in appearance from the perspective of birds, who were once dominant browsers in New Zealand. The leaves of smaller, juvenile plants are highly variable in size and shape and are mottled brown in color from the perspective of birds, which would make them difficult for herbivorous birds to locate against a background of leaf litter. However, once plants grow to above 3 m in height, beyond the reach of the largest herbivorous bird known to inhabit New Zealand, plants suddenly produce leaves that are ordinary in size, shape, and color. Results provide quantitative support for the hypothesis that *E. hookerianus* is cryptically colored when within reach of flightless browsing birds.

Keywords: color, crypsis, herbivory, heteroblasty, moa, *Elaeocarpus hookerianus*.

Introduction

There is a long history of speculation that some plants are colored and shaped in ways that make them difficult to be located by predators. For example, the size and shape of leaves produced by many species of Australian mistletoes match their hosts, which may make them difficult for herbivores to distinguish (Barlow and Weins 1977; Canyon and Hill 1997). Similarly, stone plants (*Lithops* spp.) that grow in arid, rocky habitat in southern Africa closely resemble small pebbles, which may make them difficult for herbivorous mammals to locate (Barlow and Weins 1977; Nobel 1989). However, these and other examples of crypsis in plants have yet to be thoroughly tested, and there is little quantitative evidence for the evolution of crypsis in plants (Everard and Morley 1970; Wiens 1978; Stone 1979; Atsatt 1983; Lev-Yadun 2006; Schaefer and Ruxton 2009; but see Klooster et al. 2009).

Like most other isolated islands, New Zealand lacked herbivorous mammals before the arrival of humans and instead was home to giant browsing birds, moa. Differences between birds and mammals in foraging behavior, digestion, and vision may have promoted a suite of unusual plant defenses. Few New Zealand plants produce thorns, which are known to be effective in deterring mammal herbivory (Ehrlich and Raven 1964; Grub 1992; Lev-Yadun 2001, 2003, 2006, 2009*a*, 2009*b*; Midgely et al. 2001). On the other hand, plant species from a diverse array of phylogenetic backgrounds in New Zealand are heteroblastic, with abrupt changes in morphology during ontogeny leading to distinct juvenile and adult forms (Day et al. 1997, 1998). Many New Zealand plant species are

also divaricately branched, meaning that they produce new stems at right angles to one another, which leads to an overall matted appearance (i.e., "wire plants"; sensu Bond and Silander 2007). Moreover, many heteroblastic plant species are divaricately branched in early ontogenetic stages and then more normally branched once they grow above 3 m in height, which coincides approximately with the largest known moa (Greenwood and Atkinson 1977). Although divaricate branching may have evolved to enhance physiological performance (see Day et al. 1997, 1998; Howell et al. 2002), it may also have evolved to deter moa browsing. Bond et al. (2004) offered divaricately branched plants to emu (*Dromaius baudinianus*), a close living relative of moa that is native to Australia, and found that they were damaged less than non–divaricately branched species.

Many heteroblastic species also change color during ontogeny (Day 1998). Juvenile leaves of some species are colored mottled brown, which make them difficult for human observers to locate in leaf litter. Changes in leaf color during ontogeny have led to the hypothesis that juvenile leaves are cryptically colored to deter moa browsing (Greenwood and Atkinson 1977; Brown et al. 1991). However, quantitative tests of this hypothesis are rare (Fadzly et al. 2009), and there are alternate explanations for juvenile leaf colors (Cockayne 1912; Godley 1985; Gould 1993; Kelly 1994).

Elaeocarpus hookerianus Raoul displays one of the most striking heteroblastic changes in morphology of any New Zealand tree species (Day et al. 1998). Juvenile plants are divaricately branched and produce leaves that are stunningly variable in morphology, ranging from obovate with smooth edges to linear-lanceolate with heavily serrated margins (Day et al. 1997). Juvenile leaves are also strangely colored to human observers and range in hue from pale brown to almost black in appearance. When plants grow to a height of ∼3 m, they undergo a sudden shift to a more normal appearance

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(Allan 1961). Adult plants branch at narrower angles and produce leaves that are larger and more consistently elliptical in shape than the juvenile leaves. They are also green in coloration, similar to other common tree species.

We conducted a series of morphological and spectrographic analyses to evaluate whether heteroblastic changes in the morphology of *E. hookerianus* could have evolved to deter avian browsers. First, we compared the spectral properties of seedling leaves to leaf litter to test whether they are cryptically colored from the perspective of birds. Second, given that leaf litter is comprised of a diverse array of objects—including twigs, rocks, and decomposing leaves—we tested whether juvenile leaves are more variable in size and shape than their adult counterparts, which may have made them more difficult to locate against variable leaf litter backgrounds.

Material and Methods

All data were collected from Nelson Lakes National Park, South Island, New Zealand (41°81′S, 172°85′E). Ten leaves were randomly selected from 10 juvenile plants (<300 cm tall) and 10 adult plants (>300 cm tall). We chose this height to delineate juvenile and adult plants because it appeared to be the height at which plants switched from producing juvenile to adult morphological characteristics and has been recorded previously in the literature (e.g., Greenwood and Atkinson 1977). Ten reflectance measurements of leaf litter (i.e., dead leaves, earth, rocks, and fallen branches) were collected in 10 random locations within old-growth forest (Uy and Endler 2004) and were averaged before analyses.

Leaf spectra were measured with a USB Ocean Optics 2000 spectroradiometer and Xenon Pulse X2 lamp Ocean Optics light source. An object's reflectance properties were measured as the proportion of a diffuse reflectance standard (Teflon coated white standard). The fiber optics probe was mounted inside a matte black plastic tube to exclude ambient light. The distance between each object and the probe was fixed at 1 cm, with the angle of illumination and reflection fixed at 45° to minimize glare. Irradiance was measured with a cosine corrected sensor and a D65 (normal daylight) light bulb as a reference. Spectra were calculated at 5-nm intervals from 300 to 700 nm with SpectraSuite software.

We used an eye model based on the spectral sensitivities and receptor noise of the four avian cone types (u, s, m, and l). We quantified the appearance of leaves using the contrast comparison method, which follows simple color pattern measures related to photon capture (Vorobyev et al. 1998; Endler and Mielke 2005). A detailed explanation of the mathematical formulation model is given elsewhere (Osorio and Vorobyev 1996; Vorobyev et al. 1998), but they are sufficient to predict the discriminability of any two of spectra, provided that only receptor spectral sensitivities and noise can be estimated. The calculation provides photon capture values for each type of cone receptor in the bird's eye. The receptor spectral sensitivity values were obtained from Endler and Mielke (2005) for both the *U* and *V* avian cones. Since exact spectral discrimination data are not available for moa, we used the *V* model on the basis of its closest living relative, the ostrich (*Struthio camelus*). We chose to use the ostrich because of its close phy-

logenetic relation to moa and widespread evolutionary conservatism in avian color vision (Odeen and Hastad 2003; Turvey et al. 2005).

Color can be defined as a point in a perceptual space whose coordinate axes represent quantum catches of optical receptors (Poirson and Wandell 1990). Color perception is comprised of two components, chromatic (spectral distribution) and achromatic (brightness of all wavelengths) contrasts between an object and its visual background. For chromatic comparisons, we used Endler and Mielke's (2005) analytical technique. The outputs for each of the four retinal cones (u, s, m, and l) were transformed into points in tetrahedron with a height of 1, resulting in x, y, and z Cartesian coordinates in three-dimensional space (Aitchison 2003). The chromatic contrast (C) between any two samples (e.g., leaf a and background b) are then calculated as the Euclidean distance between the two points in tetrahedral color space:

$$C = \sqrt{(x_a - x_b)^2 + (y_a - y_b)^2 + (z_a - z_b)^2}.$$

Greater Euclidean distances between points indicate greater color contrasts and a more visually apparent object. Since the height of the tetrahedron is set to 1, values range from 0 (indicating no contrast at all) to 1 (highest contrasting color).

We used a different analytical technique to make achromatic comparisons because the exact working nature of achromatic signals in birds is still poorly understood (Campenhausen and Kirschfeld 1998; Osorio et al. 1999; Hart 2001). Birds possess "double cones" that have broad spectral sensitivities that overlap with both long- and medium-wavelength-sensitive cones and are used in achromatic signal processing (non-color-based tasks; Hart et al. 2000; Jones and Osorio 2004; Cuthill 2006). Achromatic (ΔS) contrasts were calculated as

$$\Delta S = \left| \frac{\Delta f_i}{\omega_D} \right|,$$

where Δf_i is the difference in the stimulus of receptor mechanisms between signals (refer to Osorio and Vorobyev 1996; Vorobyev et al. 1998) and ω_D is the value of double cones. Because ω_D is the same for all targets, it does not affect relative achromatic contrasts. We used the only available data on double cone receptor sensitivity, which is based on red-billed *Leiothrix* (*Leiothrix lutea*), where ω_D is valued at 0.05. Discriminability of any two objects is described by the "distance" (ΔS) between them in units of "just noticeable differences" (JND). A JND value of 1 is at the threshold of discrimination. Increasing JND values indicate increasing ease of distinction, whereas values less than 1 JND are unlikely to be discriminated.

To test the hypothesis that *Elaeocarpus hookerianus* juveniles are cryptically colored from the perspective of birds against leaf litter backgrounds, we compared the chromatic and achromatic contrasts of juvenile and adult leaves against leaf litter using a general linear model. Euclidean distances in tetrahedral color space and JND values were used as dependent variables and life stage (adult vs. juvenile) was considered a fixed factor in separate analyses. Because multiple leaves were sampled from each plant, individual plants were also included in the model as a random factor to account for

the independence problem associated with sampling multiple leaves from the same individual.

To test whether juvenile plants show greater morphological variability than adult plants, we quantified the size and shape of 10 leaves from each of 10 juvenile and 10 adult plants, leading to an overall sample size of 100 leaves from each life-history stage. We scanned each leaf electronically using a flatbed scanner and then used ImageJ software (Abramoff et al. 2004) to calculate total leaf area, circularity, length to width ratio, and the dissection index, which characterizes leaf lobbing (McLellan and Endler 1998). Next we used the technique described by Beaumont and Burns (2009) to test whether morphological variability is higher in juveniles than adults. We used multidimensional scaling (PROXSCAL) to transform these four variables into two dimensions, such that points situated close together in multivariate space represent morphologically similar leaves, while points that are widely separated represent morphologically divergent leaves. To test whether adult leaves were more variable morphologically than juvenile leaves, we conducted a t-test to compare the Euclidean distances from each leaf to the centroid of their respective ontogenetic grouping. All data were log transformed when necessary to improve normality, and all analyses were conducted in R (R Core Development Team 2008).

Quantitative comparisons between the morphology of juvenile leaves and leaf litter would provide a valuable additional test of the hypothesis that heteroblastic changes in the morphology of *E. hookerianus* has evolved to deter avian browsers. However, leaf litter is comprised of a variety of very different objects, including dead leaves, twigs, stones, and soil. Although the measurements used to quantify leaf morphology (length, width, area, circularity, and lobbing) can be made accurately on recently abscised leaves, much of the leaf litter is comprised of heavily decomposed leaves, which are often loosely stuck together in brittle mats. Many decomposed leaves are also contorted in three dimensions and have large open spaces where the lamina has rotted away from the midvein. These attributes of decomposing leaves render accurate, quantitative comparisons with healthy juvenile leaves intractable. Quantifying the length, width, area, and lobbing of twigs, stones, and soil in a way that can be compared quantitatively with live leaves is also impossible, rendering quantitative comparisons between juvenile leaves and leaf litter impossible.

Results

The average reflectance curve for *Elaeocarpus hookerianus* juvenile leaves was similar to the average reflectance curve for leaf litter (fig. 1). Juvenile leaves had significantly lower chromatic contrasts (0.21 ± 0.11) with leaf litter than the adult leaves (0.53 ± 0.12) on the basis of Euclidean distances in tetrahedral color space ($F = 65.20$, df $= 1$, $P < 0.001$). Juvenile leaves also showed lower achromatic contrasts (-4.50 ± 22.08) compared with the adult leaves (11.17 ± 12.20) on the basis of JND values ($F = 7.60$, df $= 1$, $P = 0.01$).

Juvenile leaves were more variable in size and shape than adult leaves (fig. 2). Like all multivariate procedures, multidimensional scaling seeks to reduce a large number of variables (four in our case) into two dimensions, which inevitably results in the loss of information. An inverse goodness-of-fit measure called "stress" can be used to determine the accuracy of the two dimensions in describing variability in the original four variables. In this instance, normalized raw stress
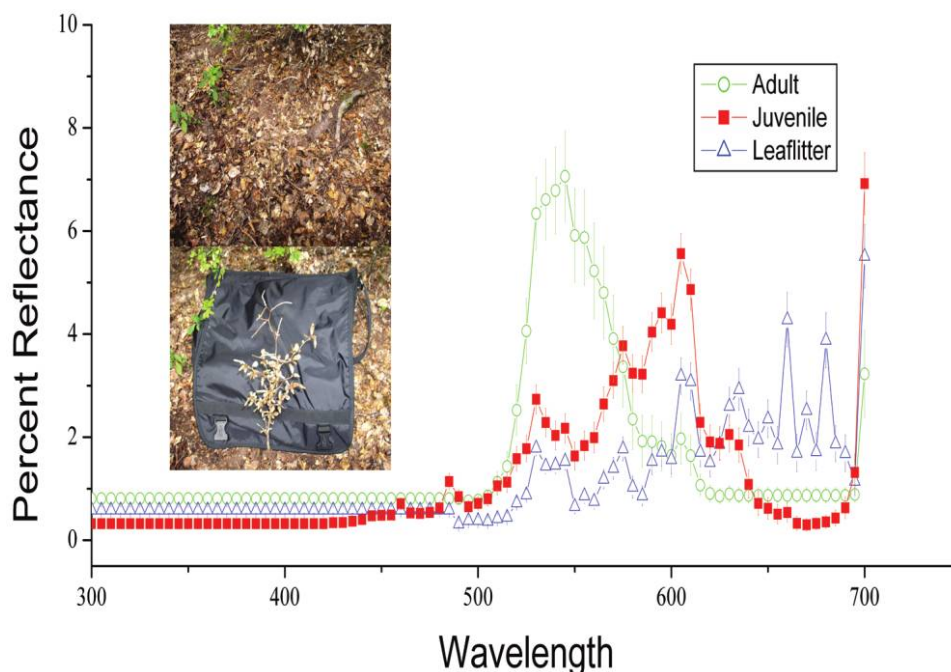

Fig. 1 Average reflectance curves (with standard error lines) for the adult and juvenile *Elaeocarpus hookerianus* and the leaf litter background. Inset shows two photographs of a single seedling taken from the same location after changes in its background.
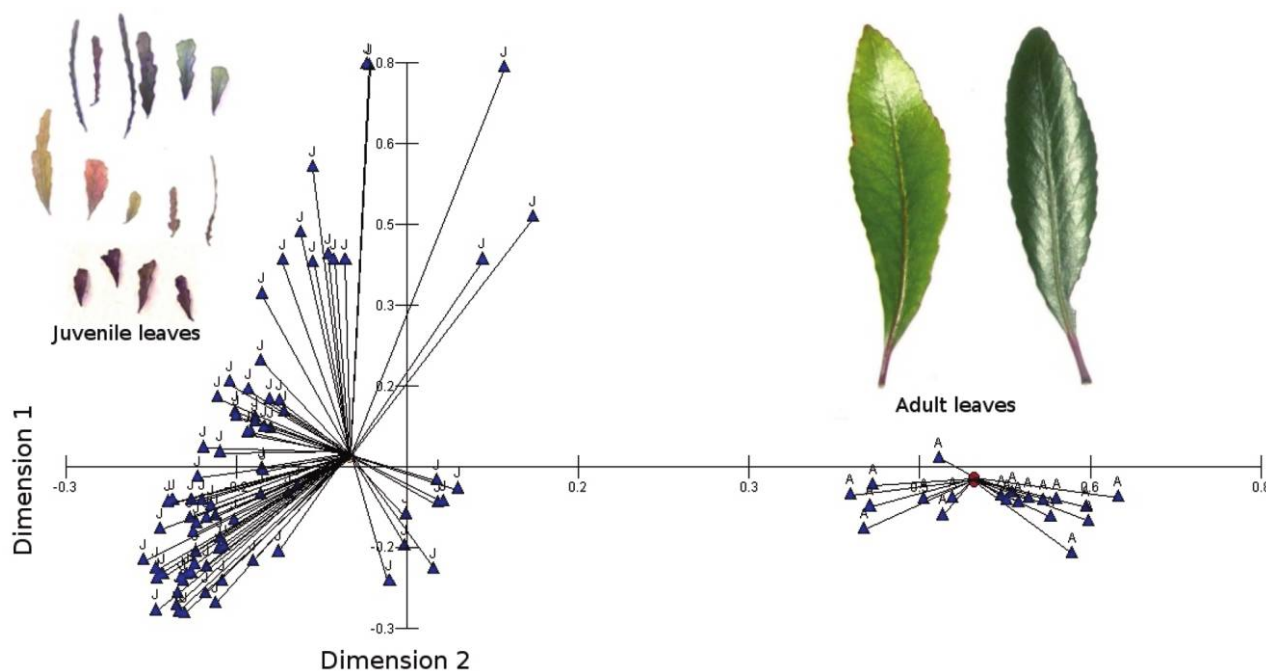
Fig. 2 Multidimensional scaling analyses (A = adult leaves, J = juvenile leaves). Lines are distances between each sample to their group centroid. Juvenile leaves (left inset) have a varied leaf shape pattern compared with the typical adult leaves (right inset).

was 0.1, indicating that the two dimensions generated by the multidimensional scaling analysis provided an accurate representation of leaf size and shape (see Sturrock and Rocha 2000). Juvenile leaves exhibited greater variability in their multivariate distributions than adult leaves, which instead formed a tight cluster of points in multidimensional space. Euclidean distances between each leaf and the centroid for its ontogenetic group were higher in juvenile leaves than adult leaves (t-test = −5.93, df = 198, P = 0.01), indicating that juvenile leaves had higher leaf shape diversity.

Discussion

Results are consistent with the hypothesis that heteroblasty in *Elaeocarpus hookerianus* evolved as a defensive strategy to deter moa browsing. Juvenile leaves displayed low chromatic and achromatic contrasts against litter backgrounds, which likely made them difficult for moa to locate. Results also showed that juvenile leaves were highly variable in both size and shape. Given that leaf litter is composed of a variety of objects that are highly variable in size and shape, morphological variability may have contributed to the cryptic appearance of juvenile leaves. However, there are other plausible explanations for heteroblastic changes in morphology (see Cockayne 1912; McGlone and Webb 1981; Godley 1985; Kelly 1994; Gamage and Jesson 2007), so this explanation for our results remains speculative.

There are many putative examples of reduce visual apparency in the New Zealand flora (see Burns 2010). For example, *Celmisia lyalli* and *Celmisia petrei* appear to mimic structurally defended species of *Aciphylla*, and *Parsonia capsularis* leaves look strikingly similar to dead twigs to the

human eye (Brown et al. 1991). However, until recently, quantitative tests for reduced visual apparency in the New Zealand flora were lacking. Fadzly et al. (2009) recently documented that *Pseudopanax crassifolius* seedlings are strikingly similar to the color of leaf litter to the avian eye, which they interpret as evidence for crypsis. However, as plants grow taller, they begin to produce long, rigid leaves with spinelike projections on their margins, which would have made them difficult for toothless browsers to swallow. Each lateral spine is also associated with a patch of brightly colored tissue, which appears to serve as an honest signal of defense (aposematism).

Similar to *E. hookerianus*, once *P. crassifolius* plants grow above 3 m in height, they begin to produce leaves that are typical in size and shape. The average spectral properties of adult leaves are also ordinary and are consistent with the reflectance properties of the primary pigments involved in photosynthesis (chlorophyll *a* and *b*), which have peak absorbance values above and below the peak in reflectance at 545 nm. However, there are several notable differences between species. First, *E. hookerianus* displays a morphological form of heteroblasty (i.e., divaricately branched juveniles) different from *P. crassifolius*, which is completely unbranched until it matures (Burns and Dawson 2009). Second, *P. crassifolius* goes through two very obvious morphological transitions during ontogeny (cryptic seedlings, aposematic saplings, and adults that are typical in appearance), while *E. hookerianus* goes through only a single transition (cryptic seedlings, typical adults; see also Day et al. 1995). Last, *E. hookerianus* displays exceptional variability in the size and shape of juvenile leaves, which is absent in *P. crassifolius* and may further enhance their similarity in appearance to leaf litter.

Klooster et al. (2009) provide another quantitative test for plant crypsis in another part of the world. *Monotropsis odorata*

is a nonphotosynthetic plant native to eastern North America that acquires carbon resources from mycorrhizal fungi (i.e., mycoheterotrophic). In the case of *M. odorata*, their reproductive structures are covered in bracts that strongly resemble leaf litter, effectively camouflaging stem and floral tissues from herbivory in a somewhat similar way to *E. hookerianus*. However, in this instance, the authors experimentally removed the bracts and showed that they effectively deter herbivores. The authors also suggest that color-based defense might be particularly common in mycoheterotrophic plants, because they do not need to use photosynthetic pigments to meet their energetic needs.

Divaricate branching, high variability of leaf shapes, and low chromatic and achromatic contrasts with leaf litter may create an isodipole texture in which visual processing cannot discriminate textures that have the same power spectrum or whose statistics are identical (Julesz 1962; Caelli and Julesz 1978a, 1978b). In this way, *E. hookerianus* juveniles may have been difficult for browsing moa to distinguish. However, crypsis is unlikely to be a fully effective defensive strategy on its own, since many animals including birds can learn to locate highly cryptic prey items. For instance, poultry chicks can be trained to pick up odd from even isodipole textures, provided there is high enough chromatic and achromatic contrast (Osorio et al. 1999; Jones and Osorio 2004).

Although these results are consistent with the moa-browsing hypothesis, other causal factors cannot be ruled out. The unique architecture of juvenile *E. hookerianus* could be a physiological adaptation to environmental conditions. Day and Gould (1997) suggest that the unusual morphology of *E. hookerianus* juveniles could be a strategy to exploit spatial variation in environmental conditions. Divaricate branching may help plants "explore" new light environments both laterally and vertically, in addition to "exploiting" previously sequestered regions within their canopy (see also Day et al. 1997). Variable leaf shapes may also have a physiological explanation. Linear-lanceolate type leaves, although costly to produce, could provide greater energetic returns to the plant if they provide better light penetration into the interior of plants, facilitating greater gas and heat exchange in the shorter, wider, obovate type leaves below (see Horn 1971; Givnish 1986; Kelly 1994).

Because moa are now extinct, the effectiveness of leaf colors in deterring moa herbivory cannot be tested directly. However, future work could be conducted on extant ratites, such as emu, as a surrogate for moa. An experimental approach similar to that of Bond et al. (2004) could be employed by manipulating leaf and background colors to test whether ratites have difficulties locating juvenile leaves that match their backgrounds, as their eye physiology suggests. These and other quantitative tests of reduced visual apparency in plants will help to establish whether crypsis is a common strategy of plant defense.

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