

DOES SELECTION FAVOR DEWLAP COLORS THAT MAXIMIZE DETECTABILITY? A TEST WITH FIVE SPECIES OF JAMAICAN *ANOLIS* LIZARDS

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ABSTRACT: Animal color signals evolve in response to selection by visual systems that perceive them, ambient light spectra that illuminate them, and features of the background against which they are juxtaposed. In *Anolis* lizards, males use a colorful dewlap, together with head-bobbing displays, to deter conspecific rivals and to attract females. As most anoles are both arboreal and sympatric with one or more congeners, selection should favor dewlap colors that contrast sufficiently with the visual background of foliage to be detectable, and that differ reliably from dewlaps of sympatric congeners to be discriminable. We used spectroradiometry and computational visual modeling for five species of closely related Jamaican anoles to calculate the detection probability of each species' dewlap in each of the species' light habitats. Despite substantial interspecific differences in dewlap colors, as well as moderate differences in habitat light spectra, results of our analyses did not support the prediction that a given species' dewlap should be more detectable in its "own" light habitat than in those of sympatric congeners. Rather, dewlaps tended to perform similarly across most light environments. Our results resemble those reported for Puerto Rican anoles, and we discuss potential reasons why *Anolis* dewlap color design does not appear to be optimized for specific light habitats.

Key words: Communication; Habitat light; Sensory drive; Signaling; Species recognition; Spectral sensitivity; Visual ecology

BRIGHTLY colored signals and ornaments are, with the exception of aposematism, thought to evolve through sexual selection and to provide advantages for attracting mates and intimidating rivals (e.g., Darwin, 1871; Andersson, 1994). As signals must first be detected before they can serve a function, selection for signal detectability, together with differences in sensory systems among intended and unintended signal receivers, may drive signal design (i.e., sensory drive; Endler and McLellan, 1988). For terrestrial organisms, the conspicuousness of ornamental coloration is a result of interactions that include the reflectance/transmittance properties of the ornament, the range and intensity of wavelengths comprising the illumination spectrum, the contrast (color and brightness) between the ornament and the visual background, and the spectral sensitivity of the viewer (Endler, 1992). Sexual selection therefore should favor colors that not only are detectable by an

intended signal receiver, but that should evolve in a manner that facilitates species recognition in cases where conspecific and heterospecific color signals may be confused. This problem of discrimination is intensified in adaptive radiations where phenotypically similar species occur in sympatry (Williams and Rand, 1977; Ryan and Rand, 1993). In guilds of related taxa, color signals that provide species identification information must not only be detectable, they also need to be discriminable from heterospecific signals (e.g., Seehausen et al., 2008).

With nearly 400 species, *Anolis* is among the most diverse genera of vertebrates in the Western hemisphere (Losos, 2009). A hallmark trait of anoles is the possession of an extensible dewlap that exhibits enormous interspecific variation (e.g., Nicholson et al., 2007). In the majority of *Anolis* species the dewlap is elaborated only in males, and is used together with headbobbing displays to attract females and to deter potential male rivals.

Anolis lizards living in different structural habitats are likely to experience dissimilar quantities and qualities of ambient illumination (e.g., Fleishman et al., 1997), and light

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conditions that vary with forest geometry (Endler, 1992, 1993) might underlie the evolution of dewlap color diversity. The correlation between illumination spectra and color signal broadcast efficacy (e.g., Endler, 1992; Endler and Théry, 1996; Gomez and Théry, 2004) predicts that certain dewlap colors should be more visible in some light environments than in others. Although Nicholson et al. (2007) found no support for the hypothesis that anoles in similar structural habitats should be more similar in dewlap color pattern configuration than that expected by chance, certain dewlap colors nevertheless tend to be associated with certain habitat light characteristics (e.g., Fleishman, 1992).

Some previous research has examined the potential relationships between environmental variables and variation in a species' dewlap coloration across its distribution. For example, on Puerto Rico, Leal and Fleishman (2004) found dewlap coloration to be brighter and more UV-reflective in *Anolis cristatellus* from mesic habitats than xeric habitats. By comparison, Ng et al. (2012) found that dewlap coloration in *Anolis distichus* on Hispaniola was brighter in xeric than in mesic habitats. Also in contrast to Puerto Rican anoles (e.g., Fleishman et al., 1993), Ng et al. (2012) did not find a consistent relationship between UV reflectance and habitat type in *A. distichus* on Hispaniola. Determining the causes of the differences in these two sets of findings awaits future research.

Dewlap signal design has been examined for several species within a given *Anolis* radiation (e.g., Fleishman et al., 1993, 1997, 2009). Most pertinent to the present study, Fleishman et al. (2009) asked whether differences in light habitats of four Puerto Rican anoles were sufficient to explain interspecific differences in dewlap coloration. Based on earlier findings (i.e., Leal and Fleishman, 2002, 2004), these authors predicted that if dewlap colors have diverged because of increased detectability in particular light environments, then a given species' dewlap should be more detectable in its own light environment than should the dewlaps of its sympatric congeners. Instead of supporting this prediction, however, the rank order of detectability for the four species' dewlaps was similar in each species' habitat

(Fleishman et al., 2009). The authors concluded that selection probably places the broadest constraints on dewlap colors that can be readily detected within a given light habitat, and that additional variables, such as species recognition (e.g., Losos, 1985; Macedonia and Stamps, 1994; Macedonia et al., 2013), must influence the dewlap phenotype. Other factors include the possibilities that (1) dewlap detectability might more tightly constrain the range of highly visible colors in some habitats (e.g., low light intensity) than in others; (2) selection might favor dewlap colors in sympatric species that diverge from each other, and hence potentially away from detectability optima; and (3) counterselection for dewlap detectability might occur via the spectral sensitivity of anole predators and prey (Fleishman et al., 2009).

To assess the general applicability of the findings for dewlap detectability in Puerto Rican anoles, comparative data are needed from *Anolis* radiations on the other three Greater Antillean islands (i.e., Cuba, Hispaniola, and Jamaica). As a starting point, we replicated the study of Fleishman et al. (2009) with the use of members of the "*Anolis grahamsi* series"—an independent, monophyletic radiation of anoles on Jamaica (e.g., Jackman et al., 2002; Fig. 1). To ensure that our results would be directly comparable to those of Fleishman et al. (2009), our data acquisition and analysis methods, as well as our graphical presentation of results, mirror those of these authors as closely as possible. We did not replicate every data analysis carried out by Fleishman et al. (2009), but instead chose analyses that we felt were most important for comparing the Puerto Rican and Jamaican anole faunas.

In this study, we used spectroradiometry to measure dewlap reflectance and transmittance, and to characterize the ambient light and visual backgrounds for each of our five study species. We used computational visual modeling, based on the spectral sensitivities of each species, to calculate brightness contrast and chromatic contrast of each dewlap against the visual background of each light habitat. We then employed these quantities to determine the probability of detection, $P(d)$, of each species' dewlap in each species' light

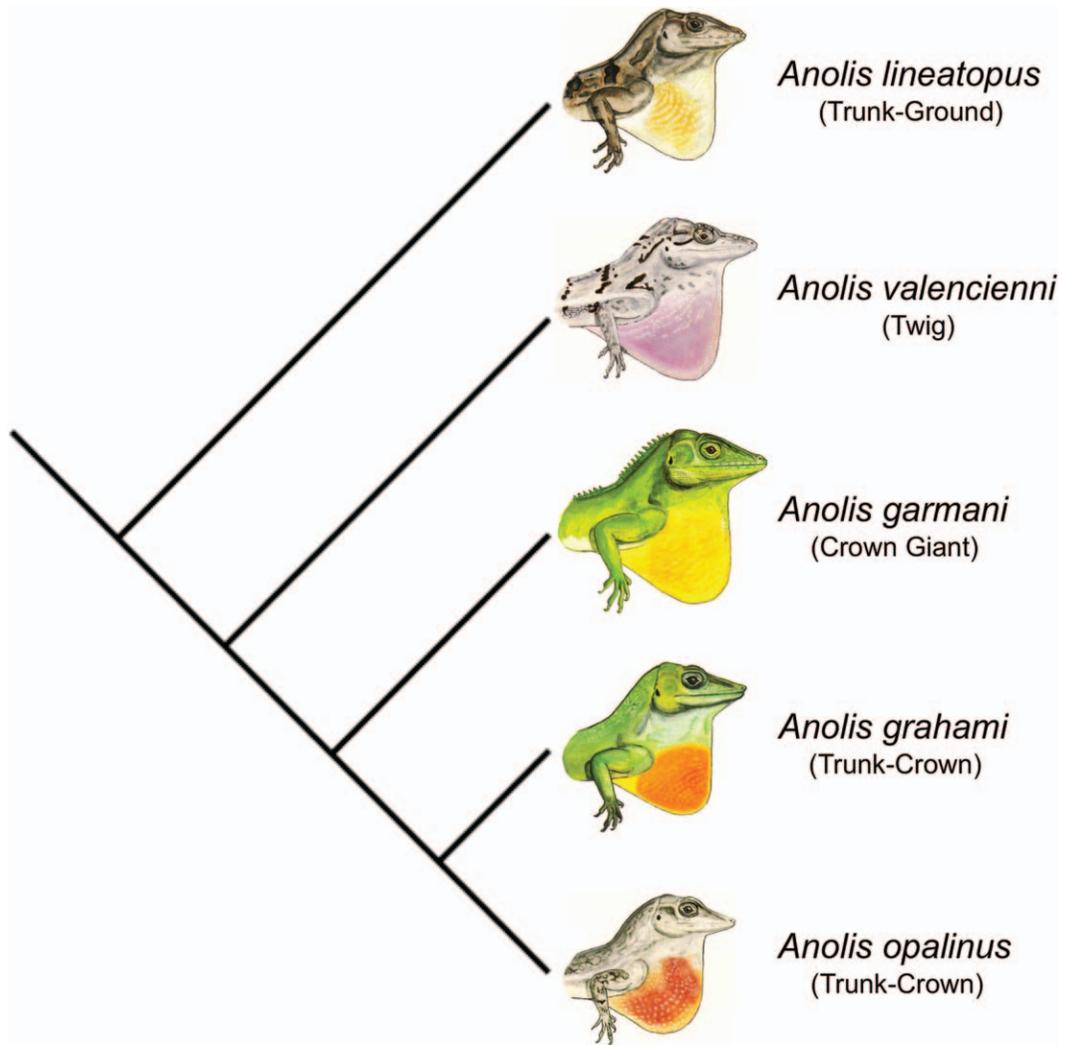


FIG. 1.—Cladistic relationships of five Jamaican members of the *Anolis grahami* series, including their structural habitat classification, scaled for relative size. (Images used with permission.)

habitat. Following Fleishman et al. (2009) we hypothesized that if dewlap color design is a product of selection that maximizes detectability, then each species' dewlap color should exhibit a greater $P(d)$ in its own light habitat than should those of its sympatric congeners.

Although much research has been aimed at uncovering factors that affect dewlap size, as well as the information that dewlap size variation might convey (e.g., Losos and Chu, 1998; Vanhooydonck et al., 2005; Lailvaux and Irschick, 2007), our study does not consider the potential effects of absolute dewlap size on

dewlap detectability. We expect that, all else being equal, dewlap size and detectability should scale together (i.e., a larger dewlap should be more detectable than a smaller one).

MATERIALS AND METHODS

Study Area and Species

The *A. grahami* series is a monophyletic radiation of seven species, six of which are endemic to Jamaica (e.g., Williams, 1976; Jackman et al., 2002; Fig. 1). The seventh

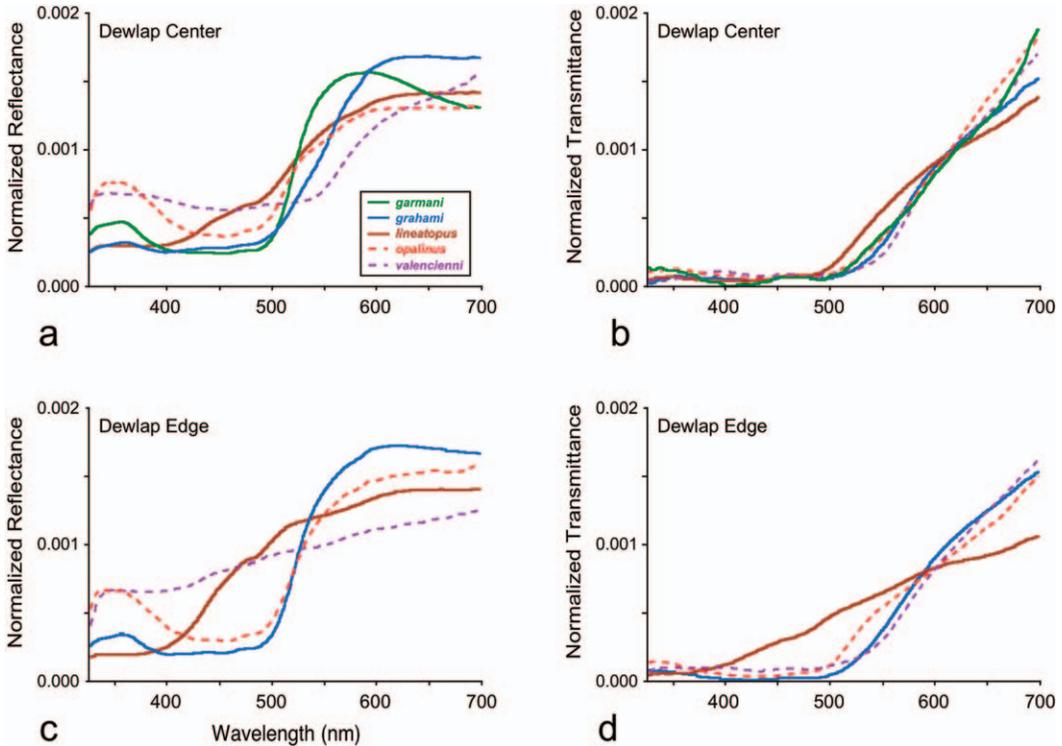


FIG. 2.—Normalized dewlap center and edge reflectance and dewlap transmittance of the five study species from 325 to 700 nm. The area under each curve sums to 1. Legend: *Anolis garmani* (green solid line), *Anolis grahami* (blue solid line), *Anolis lineatopus* (brown solid line), *Anolis opalinus* (red dashed line), *Anolis valencienni* (purple dashed line). Sample sizes: *A. garmani* (center: $N = 5$), *A. grahami grahami* (center: $N = 10$; edge: $N = 5$), *A. lineatopus merope* (center: $N = 8$; edge: $N = 8$), *A. opalinus* (center: $N = 5$; edge: $N = 2$), *A. valencienni* (center: $N = 6$; edge: $N = 6$). The dewlap edge was not measured in *A. garmani*, as the entire dewlap is uniform in color. (A color version of this figure is available online.)

species, *Anolis conspersus*, evolved on Grand Cayman as the sister to *A. grahami* from southern and central Jamaica (Grant, 1940; Macedonia, 2001; Macedonia and Clark, 2001; Jackman et al., 2002).

We collected spectral data over a 2-wk period in May 2008 at the Discovery Bay Marine Lab (DBML, University of the West Indies, Discovery Bay, Jamaica) and in surrounding locations. This habitat is tropical dry limestone (“ironshore”) forest, in which the following *Anolis* species occur (mean \pm 1 SE snout-vent lengths [SVL], from Losos, 2009): *Anolis garmani* (109.3 ± 1.50 mm), *A. grahami* (61.6 ± 0.93 mm), *Anolis lineatopus* (57.2 ± 0.51 mm), and *Anolis valencienni* (72.1 ± 1.69 mm). Our fifth study species, *Anolis opalinus* (SVL = 47.7 ± 0.47 mm), does not occur on the grounds of the DBML.

Therefore, light habitat data for *A. opalinus* (as well as supplemental spectral data for our other study species) were gathered in Ocho Rios, approximately 40 km east of Discovery Bay.

Definition of Terms

In this study we define light “intensity” as the sum of individual wavelength amplitudes over a specified set of wavelengths. By comparison, “brightness” is perceived intensity, which is dependent on the spectral sensitivity of the viewer. “Color” refers to the spectral distribution of light independent of intensity; color is comprised of hue and chroma. “Hue” is defined by the shape of the spectral reflectance curve, and especially by its peak. “Chroma” is color saturation, and is a function of the relative difference in magni-

tude between adjacent high- and low-amplitude wavelengths in a reflectance or radiance spectrum. “Irradiance” is the spectral sum of light from a hemisphere striking a flat surface over a defined range of wavelengths, and is measured in photons as $\mu\text{mols m}^{-2} \text{s}^{-1} \text{nm}^{-1}$. “Spectral irradiance” is irradiance per unit wavelength. “Radiance” is the spectral sum of incident light reflected from an object as measured over a small solid angle in photons as $\mu\text{mols m}^{-2} \text{s}^{-1} \text{nm}^{-1} \text{sr}^{-1}$ (where sr = steradians). “Spectral radiance” is radiance per unit wavelength. “Reflectance” refers to the distribution of light reflected from an object over a defined range of wavelengths with respect to a virtually perfect matte reflector (i.e., a white standard). “Brightness contrast” is the perceived intensity difference between an object and the background, whereas “chromatic contrast” refers to perceived color differences between object and background spectra that are independent of intensity. We define wavelengths from 600–700 nm as long wavelengths, those from 500–600 nm as middle wavelengths, those from 400–500 nm as short wavelengths, and those below 400 nm as ultraviolet (UV) wavelengths.

Measurement of Dewlap Spectra

We measured dewlap radiance in a darkened laboratory room at the DBML. Subjects were secured to a micromanipulator with a belt of Velcro® and their dewlaps were opened fully from the front edge by a pair of stabilized forceps. A deuterium-tungsten light source (Model DT-Mini, Analytical Instrument Systems, Inc., Flemington, NJ) positioned on one side of the dewlap projected a light beam that passed through a diffuser (tracing paper) and produced a spot on a subject’s dewlap ≈ 15 mm in diameter. An optical fiber, fitted with a collimating lens (“radiance probe”), was placed on the side of the dewlap opposite the light source, with the collimating lens positioned directly in the center of the spot of light. A second radiance probe was placed on the same side of the dewlap as the illumination source, and was oriented at an angle approximately 70° to the dewlap plane. This angle approximates a direct line of sight by a lizard to the dewlap, without blocking the illumination source

(Fleishman et al., 2009). Prior to being positioned at a subject’s dewlap, collimating lenses had been adjusted to a 2° acceptance angle. The field of view of each collimating lens was aligned to the dewlap center (or edge) by shining a laser pointer through the optical fiber and lens and onto the dewlap.

Three types of spectral measurements were made once the fibers had been secured in place. First, we obtained the spectrum of the beam reflecting from the same side of dewlap as the light source. Next, we obtained the spectrum of the beam transmitted through the dewlap. Last, the lizard was removed from the holder and the direct beam from the lamp (through the diffuser) was obtained. The dewlap center was measured for at least five adult males of each species (as in Fleishman et al., 2009). Subjects then were repositioned slightly so that each radiance probe was focused on the dewlap edge. The dewlap edge was not measured for *A. garmani*, as the entire dewlap is uniform in color.

For each reflected and transmitted radiance spectrum, we produced a radiance/irradiance ratio (R/I) ratio at each wavelength (e.g., Leal and Fleishman, 2004). Dividing dewlap radiance by the illumination spectrum (= irradiance) from the same side as the light source produces a dewlap reflectance spectrum, and dividing dewlap radiance by the illumination spectrum from the transmitted side of the dewlap results in a transmission spectrum (Fig. 2). Summing these two quantities together provides a complete R/I ratio. This computation can be used to estimate total dewlap radiance in any light environment by multiplying the ratio by a given habitat irradiance spectrum. The R/I ratio therefore allows us to test the broadcast efficacy of a given dewlap color in a given light habitat (see Leal and Fleishman, 2004, for details).

Measurement of Habitat Light Spectra

Results from prior studies failed to reveal differences in ambient light spectra between locations where anoles displayed their dewlaps and randomly selected locations (e.g., Leal and Fleishman, 2004; Fleishman et al., 2009). Therefore, we collected our habitat light spectra wherever adult male anoles were located, whether or not they were displaying.

Samples were gathered at all times of day but were restricted to times when the sky was more than one-third blue and the sun was not obscured by clouds (after Fleishman et al., 1997).

For all spectral sampling we used Ocean Optics (Dunedin, FL) USB 4000 or USB 2000+ spectrometers and fiber optic cables, connected to laptops running Ocean Optics SpectraSuite software. Two types of probes, one for sampling habitat irradiance and the other for sampling habitat radiance, were attached to the end of an extendable pole. Although most anoles were observed on tree trunks at 1–2 m above the ground, the pole apparatus allowed us to sample locations up to approximately 5 m above the ground. Once a subject was discovered and was observed for about a minute, the end of the pole was positioned precisely at the location in the tree that the lizard had occupied. All light samples were obtained with probes pointed parallel to the ground, and were gathered in each direction that the lizard's eyes had been facing (i.e., left and right). Unlike Fleishman et al. (2009), we did not gather additional samples of habitat radiance at an angle 45° upward relative to parallel with the ground.

Side-welling irradiance represents the ambient light spectrum that is illuminating the target (dewlap) laterally, and was measured using a cosine-corrector (Ocean Optics CC-3-UV) that gathers light over a 180° hemisphere. Prior to obtaining readings each day, irradiance was calibrated with the use of SpectraSuite with a light source (LS-1-CAL) designed for this probe. Side-welling radiance, which represents a small target falling on the retina at eye level, was obtained with the use of a collimating lens (Ocean Optics 74-UV) adjusted to a 4° acceptance angle. Radiance was calibrated with the use of the bare optical fiber with the LS-1-CAL and SpectraSuite. All habitat light samples were converted to quantal units (irradiance: $\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1}$, radiance: $\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1} \text{sr}^{-1}$) before being analyzed. To obtain representative habitat light irradiance and radiance spectra for each species, the left-side and right-side irradiance samples were averaged for each lizard, and a grand mean was calculated. Among-species comparisons of

irradiance spectra and radiance spectra were carried out with one-way ANOVAs. When comparisons were significant, post-hoc between-species pairwise tests were conducted with the use of protected Sheffé *F*-tests.

Visual Modeling

Anoles possess four classes of visual pigments: long-wavelength-sensitive (LWS), middle-wavelength-sensitive (MWS), short-wavelength-sensitive (SWS), and UV-wavelength sensitive (UVS). We generated Gaussian absorbance curves for each of the four visual pigments (cone classes) in each of our five study species with the use of the template of Govardovskii et al. (2000). Mean visual pigment absorbance peak values (λ_{max}) used in these calculations can be found in Loew et al. (2002). Each cone class also possesses an associated oil droplet that filters light prior to its absorbance by a visual pigment. To model the absorbance spectrum of each oil droplet type, we entered the mean peak absorbance value of the oil droplet associated with a given visual pigment (from Loew et al., 2002) into a template created for this purpose (i.e., Hart and Vorobyev, 2005). We then multiplied the inverse of the oil droplet absorbance (i.e., the droplet transmittance) by its associated visual pigment absorbance spectrum to estimate total photoreceptor absorbance for each cone class of each study species.

Given that birds, reptiles, and amphibians assess brightness with the use of “double cones” (e.g., Siddiqi et al., 2004), an estimate of the spectral sensitivity for each species' double cone was used in brightness contrast (C_b) calculations. Each double cone contains a principal member with a yellow oil droplet (indistinguishable from the yellow oil droplet associated with the LWS cone) and an accessory member that lacks the oil droplet but contains a dispersed yellow pigment of variable density (Loew et al., 2002). We modeled the absorbance spectrum of the double cone as the mean of the absorbance of the LWS cone containing the oil droplet and the absorbance of the LWS cone lacking the oil droplet.

Generating dewlap-background brightness contrast and chromatic contrast values were a prerequisite to determining the probability of

detection, $P(d)$, of a given species' dewlap in a given light habitat. We followed Fleishman et al. (2009) in our calculations of brightness contrast, chromatic contrast, and adapting stimulus. Brightness contrast was calculated for each subject in its own light habitat and in the light habitats of its four sympatric congeners, and was computed as

$$B_c = (B_s - B_b)/(B_s + B_b)$$

where B_s is stimulus (dewlap) brightness and B_b is background brightness. Brightness contrast in anoles has been shown (Fleishman and Persons, 2001) to be restricted to the wavelength range of 450–700 nm, and this is the range over which we calculated brightness contrast in this study. As brightness is perceived logarithmically, irradiance and background radiance were $\log + 1$ transformed prior to brightness contrast calculations. Values greater than zero indicate that dewlap radiance is brighter than background radiance, whereas values less than zero indicate that dewlap is darker than the radiance of the background.

To calculate chromatic contrast we used the cone class spectral sensitivities for the species whose dewlap radiance we were measuring, together with paired irradiance and background radiance samples gathered at each subject's location. For example, when modeling the appearance of the *A. garmani* dewlap (to its own visual system) in *A. lineatopus* habitat light, *A. garmani* spectral sensitivity and total dewlap radiance were used together with a sample of paired *A. lineatopus* habitat irradiance and background radiance. We multiplied a given species' mean normalized dewlap radiance (i.e., R/I ratio \times a given habitat irradiance) by each chromatically adapted cone class in that species. The output for each cone class was expressed as a proportion of the sum of all four outputs, which together sum to 1. We then carried out the same calculations for the background radiances.

Chromatic contrast was computed as

$$C_C = \left[(S_{UVS} - B_{UVS})^2 + (S_{SWS} - B_{SWS})^2 + (S_{MWS} - B_{MWS})^2 + (S_{LWS} - B_{LWS})^2 \right]^{1/2},$$

where S is the stimulus (dewlap) radiance and B is the background radiance. This quantity represents the Euclidian distance between two points (dewlap and background spectral radiance) in four-dimensional space, and can be plotted in a color tetrahedron (e.g., Macedonia et al., 2009).

We used the mean side-welling irradiance spectrum for each species as the adapting stimulus for that species' light habitat. We then multiplied this quantity for each species by each cone class/oil droplet absorbance spectrum (i) of that species to produce a correction factor k_i (i.e., von Kries adaptation; Fleishman et al., 2009). In our calculations of dewlap-background chromatic contrast, the output of each cone class therefore was multiplied by $1/k_i$ to account for viewing a stimulus in the same ambient light spectrum to which the photoreceptors are adapted.

Dewlap Probability of Detection

The dewlap probability of detection was calculated with the use of an empirically derived equation (Fleishman and Persons, 2001):

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

where $P(d)$ is the probability of detection, $\text{ABS}(C_B)$ is the absolute value of brightness contrast, and (C_C) is the chromatic contrast between the dewlap and background radiance. This equation arises from data based on the "visual grasp" reflex of *A. cristatellus* to a moving dewlap-like stimulus, which was varied independently in brightness and hue from the background against which it was viewed (Fleishman and Persons, 2001). The spectral sensitivity of *A. cristatellus* is typical for anoles (see Loew et al., 2002), and $P(d)$ allows us to compare our results directly with those of Fleishman et al. (2009) on Puerto Rican anoles. Repeated-measures ANOVAs were used to test for $P(d)$ differences of dewlaps in different light habitats. Where significant differences were found, pairwise tests between habitats were made with protected Tukey HSD tests. Following Fleishman et al. (2009), values for $P(d)$ were arcsine-square-root transformed prior to test-

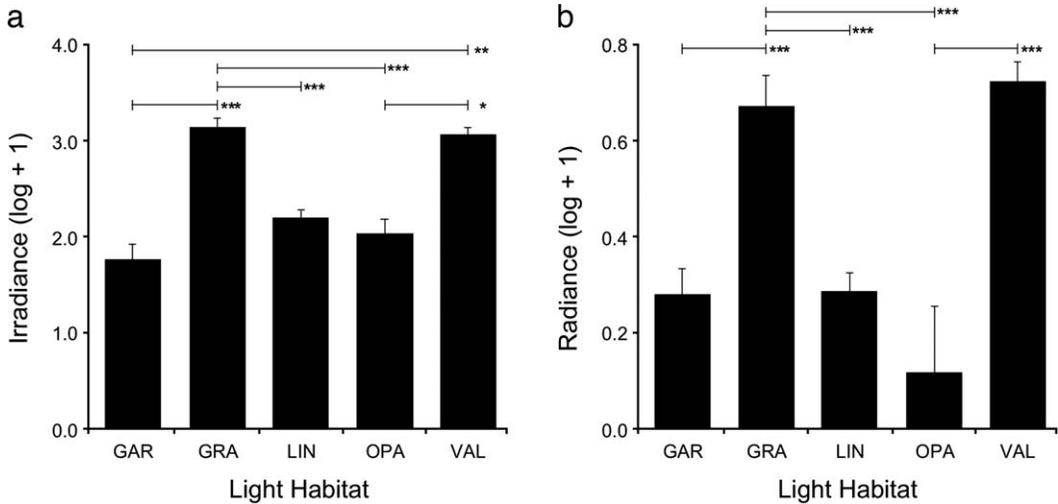


FIG. 3.—Comparison of log-transformed (a) irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1}$) and (b) radiance ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1} \text{sr}^{-1}$) in the light habitats of each of five *Anolis* species. See Methods section for details on recording light readings. Horizontal line endpoints connect significant pairs of means (+1 SE; Sheffé *F*-tests) in one-way ANOVAs conducted separately for irradiance and radiance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Species abbreviations: GAR = *Anolis garmani* ($N = 28$), GRA = *Anolis grahami* ($N = 38$), LIN = *Anolis lineatopus* ($N = 36$), OPA = *Anolis opalinus* ($N = 16$), VAL = *Anolis valencienni* ($N = 4$).

ing. All statistical tests were carried out with the use of SPSS v19.0 for Macintosh.

RESULTS

Habitat Light Intensity

Results of one-way ANOVAs on habitat light intensity revealed differences among the five species' light habitats in side-welling irradiance ($F_{119,4} = 27.12$, $P < 0.001$; Fig. 3a) and background radiance ($F_{119,4} = 16.77$, $P < 0.001$; Fig. 3b). In most cases, pairwise comparisons (Sheffé *F*-tests) revealed differences in irradiance between (but not within) two groups of species: those found predominantly in the sun (*A. grahami* and *A. valencienni*) and those usually found in the shade (*A. garmani*, *A. lineatopus*, and *A. opalinus*). Comparisons of background radiance produced similar results to those for irradiance, except that differences between the sun and shade species were larger and variance was greater (Fig. 3b). Background radiance for *A. opalinus* stood out as being particularly low and highly variable among subjects (Fig. 3b). This result might stem from the fact that we most often found *A. opalinus*

located on the shaded side of trees in sunny patches of forest.

Normalized average irradiance revealed several differences among species in spectral shape (Fig. 4a). For example, irradiance spectra for the shade-preferring *A. lineatopus* were strongest in middle wavelengths, as most sunlight was filtered through and reflected from leaves, and weaker in the short/UV and long wavelengths, as there was little open sky or direct sunlight contributing to the illumination spectrum (Fig. 4a). In contrast, irradiance spectra for the sun-preferring *A. grahami* were strongest in long wavelengths (direct sunlight) and weaker in middle wavelengths (i.e., less light filtered through leaves; Fig. 4a). Normalized average radiance spectra were much more similar among the five study species than were irradiance spectra. Radiance curves for all species were strongest in the middle wavelengths because of a foliage-dominated visual background (Fig. 4b). Nevertheless, *A. lineatopus* and *A. grahami* exhibited the same pattern of shade versus sun extremes, respectively, that we observed for habitat irradiance (Fig. 4a,b).

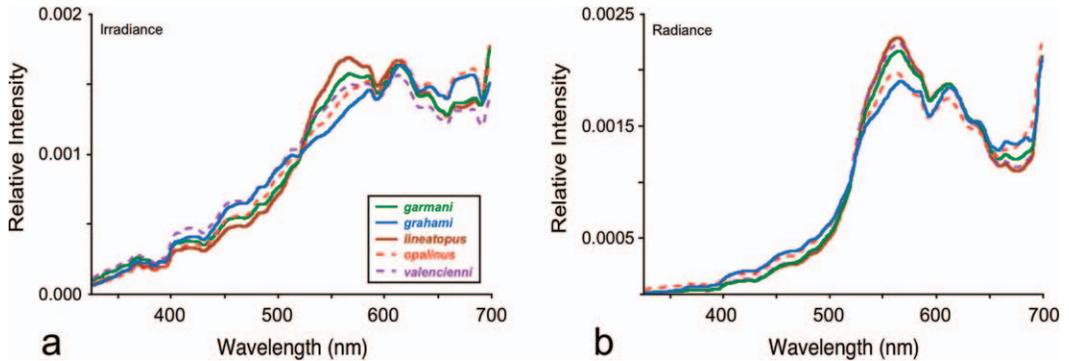


FIG. 4.—Normalized mean side-welling (a) irradiance and (b) radiance spectra in the light habitats of each of five *Anolis* species. The area under each curve sums to 1. Legend as in Figs. 2, 3. (A color version of this figure is available online.)

Dewlap–Background Contrast

Brightness contrast of the dewlap center with the visual background was greatest across light habitats for *A. garmani* and *A. valencienni*, except in *A. opalinus* habitat where contrast was strongest for *A. lineatopus* (Fig. 5, left panel). Brightness contrast of the dewlap edge with the background was greatest across light habitats for *A. valencienni* (*A. garmani* was not tested for dewlap edge; see METHODS), except in *A. opalinus* habitat, where contrast again was strongest for *A. lineatopus* (Fig. 5, right panel). Chromatic contrast of the dewlap center and edge against the visual background was greatest for *A. grahami* in all light habitats (Fig. 5).

Dewlap Probability of Detection

Repeated-measures ANOVAs on the probability of detection $P(d)$ of each species' dewlap in each light habitat were significant for all comparisons (dewlap centers: $F_{52,4} \geq 3.02$, $P \leq 0.03$; dewlap edges: $F_{9,3} \geq 5.93$, $P \leq 0.004$). In every light habitat but that of *A. valencienni*, both *A. grahami* and *A. opalinus* exhibited the largest dewlap detection probabilities for dewlap centers (Fig. 6a–d). By comparison, in *A. valencienni* habitat light, *A. garmani* and *A. valencienni* dewlap centers exhibited the largest $P(d)$ values (Fig. 6e). For dewlap edges, *A. grahami* exhibited the largest detection probabilities across all species' light habitats, although in most cases, $P(d)$ values of *A. grahami* were only slightly

greater than those of *A. opalinus* and *A. valencienni* (Fig. 6g–k).

DISCUSSION

Theory predicts that selection should shape color signals to maximize their detection by intended audiences at locations where the signals are displayed (Endler, 1992). This outcome appears to be a balance between a color signal's reflectance and transmittance, intensity and shape of the illuminating spectrum, contrast between the color signal and the visual background, and viewer spectral sensitivity. We took these factors into account to test the prediction that a given species' dewlap would exhibit a higher probability of detection in its own light habitat than would the dewlaps of its congeners. As reported for Puerto Rican anoles by Fleishman et al. (2009), our findings for Jamaican anoles did not support this prediction.

Puerto Rican and Jamaican Anoles Compared

The four species of Puerto Rican anoles studied by Fleishman et al. (2009) differed considerably in habitat light intensity, ranging from a species found uniformly in dark forest shade (*Anolis gundlachi*), to two species found in partial shade (*Anolis krugi* and *A. cristatellus*), to a species usually observed in the absence of shade (*Anolis pulchellus*). By comparison, our habitat light data effectively collapsed the two shade categories into one, leaving three shade species (*A. garmani*, *A.*

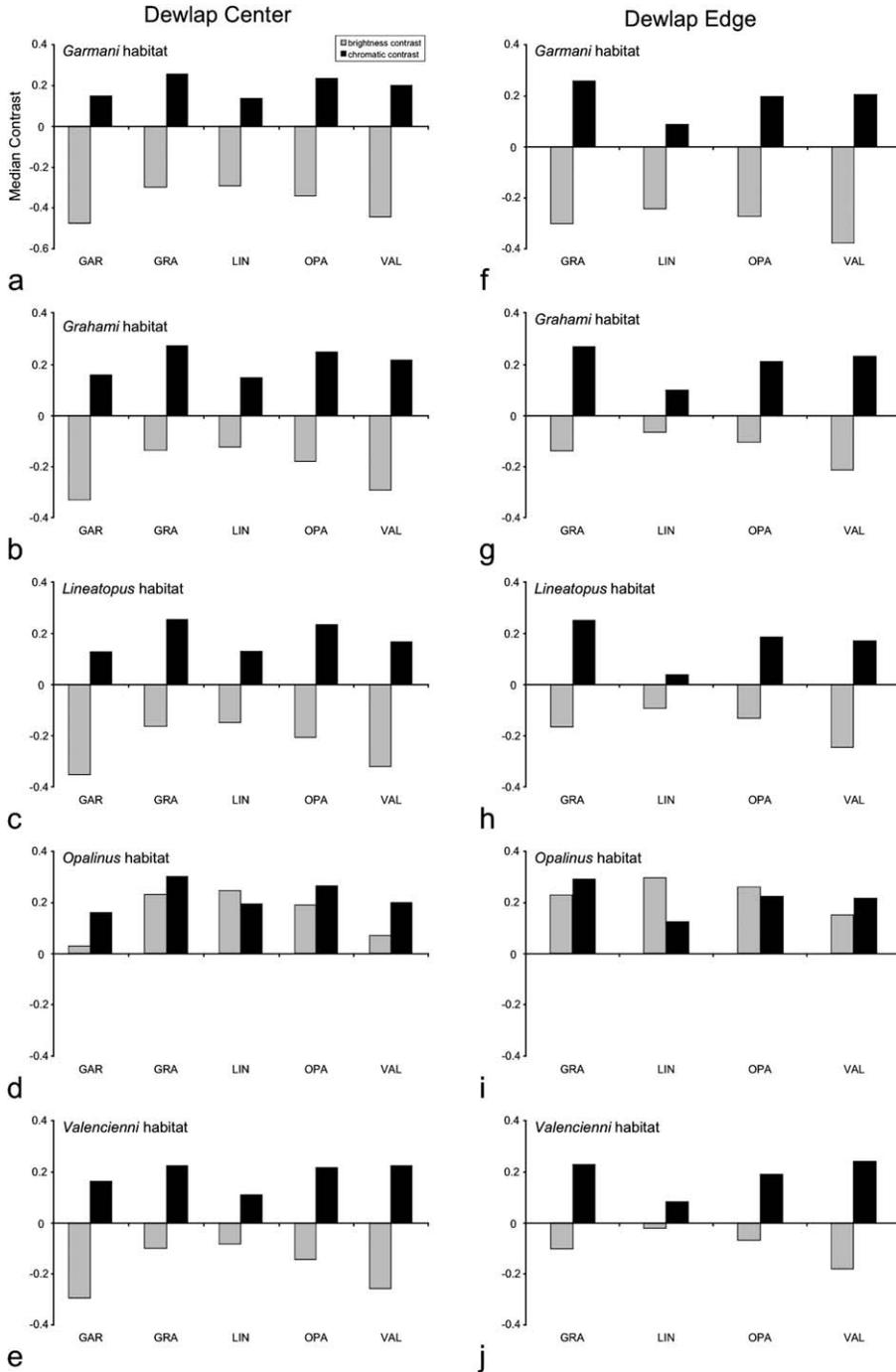


FIG. 5.—Median brightness contrast (gray bars) and chromatic contrast (black bars) of the dewlap with the visual background for each of five *Anolis* species in each light habitat. Legend as in Fig. 3.

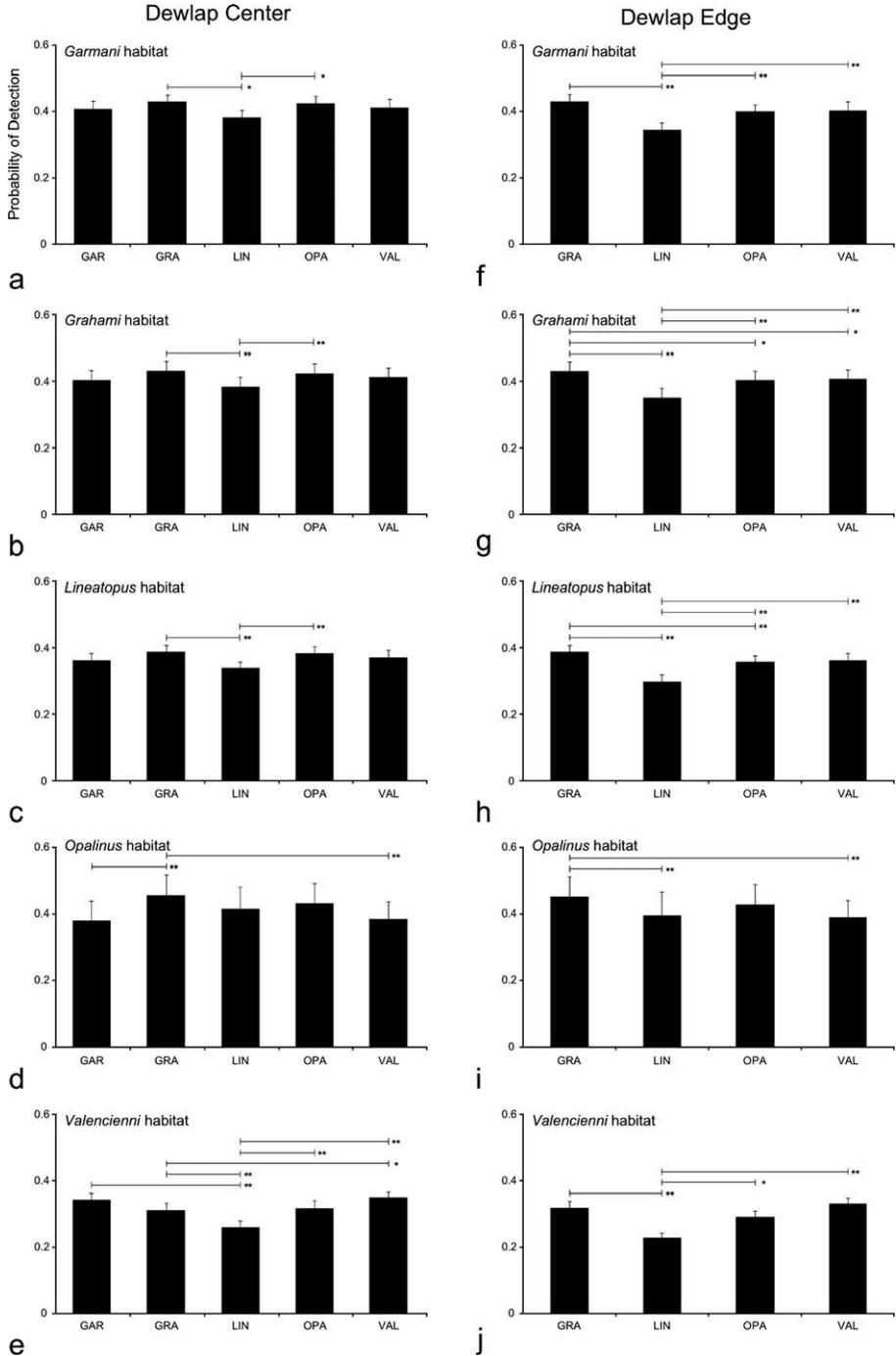


FIG. 6.—Comparisons of mean detection probability, $P(d)$, of dewlap centers and edges calculated for every location measured in the light habitat of each of five *Anolis* species. Horizontal line endpoints connect significant pairs of means ($+1$ SE; Tukey HSD) in significant repeated-measures ANOVAs conducted on dewlap centers and edges for each habitat. Detection probabilities arcsine-square-root transformed prior to statistical testing. See Methods section for $P(d)$ calculation details.

lineatopus, and *A. opalinus*) and two sun species (*A. grahami* and *A. valencienni*).

Fleishman et al. (2009) found that detection probabilities for the dewlap edges of two Puerto Rican species, *A. krugi* (pale yellow) and *A. pulchellus* (red), were similar and together were greater than the detection probabilities for *A. gundlachi* (dark amber) and *A. cristatellus* (yellow) in all four species' light habitats. By comparison, detection probabilities for the dewlap centers of two Jamaican species, *A. grahami* (orange with yellow edge) and *A. opalinus* (reddish-orange with yellow edge), were similar and greater than those of our other three study species in all light habitats except that of *A. valencienni*. In addition, detection probabilities of the dewlap edge were greatest for *A. grahami* in all light habitats except that of *A. valencienni*, where probabilities for these two species were similar.

Overall, results from the two studies were fairly consistent. In both studies, a pair of species with long-wavelength-reflective (yellow, orange, or red) dewlaps exhibited greater detection probabilities in most or all light habitats than did their sympatric congeners. Furthermore, results of both studies failed to support the prediction that each species' dewlap should be more detectable in its own habitat light than those of sympatric congeners. The lack of support for this prediction led Fleishman et al. (2009) to address the question of why relative detectability of dewlaps changes so little across light habitats that are as dramatically different as dark forests and bright open areas. The authors determined that at least three factors are responsible.

First, dewlap-background contrasts upon which $P(d)$ depend arise largely as differences between habitat irradiance and background radiance. As these two variables typically scale together within habitats, differences in light intensity among habitats have little effect on $P(d)$ (Fleishman et al., 2009). Second, chromatic adaptation to the spectral shape of habitat irradiance results in modest changes in chromatic contrast (black bars in Fig. 5), leaving chromatic contrast to depend on differences between dewlap color and background radiance (Fleishman et al., 2009).

Third, large differences in forest geometry might better explain how habitat light adaptively influences dewlap coloration (e.g., Leal and Fleishman, 2002, 2004) than do differences in light intensity and degree of shade in similar forest types (Fleishman et al., 2009).

Although dewlap detectability has played a role in the evolution of dewlap color diversity, selection for detectability in differing light habitats is insufficient to explain the variety of dewlap colors present among sympatric species assemblages. Fleishman et al. (2009) concluded that dewlap color diversification is most likely driven by multiple (and sometimes competing) factors, and that selection for species identification might explain a portion of the variation observed in dewlap color patterns observed among sympatric anoles.

The Puzzle of Anolis opalinus: A Shade Species with a "No Shade" Dewlap

An intriguing finding from our study revealed an apparent conflict in *A. opalinus* between habitat light and dewlap coloration. Despite being well documented as a shade species (e.g., Rand, 1967; Schoener, 1970; Schoener and Schoener, 1971), the densely pigmented reddish-orange dewlap of *A. opalinus* (Figs. 1, 2a), which also exhibits the strongest UV dewlap reflectance among the Jamaican anoles, seems better suited to light habitats with little to no shade (e.g., Fleishman, 1992; Fleishman et al., 1993). Complicating this matter is the fact that dewlap coloration is similar to that of *A. grahami* (Fig. 1), a strongly heliophilic species. In Ocho Rios, where we collected our habitat light spectra for *A. opalinus*, this species was most often found on the shaded side of trees in sunny areas surrounded by dark forest.

We speculate that interference competition from *A. grahami* and *A. lineatopus* (both of which are considerably larger in body size than *A. opalinus*) might partly explain the mismatch between *A. opalinus* dewlap coloration and habitat light. Throughout Jamaica *A. opalinus* is sympatric with *A. grahami*, except in areas where the latter species is absent or rare (e.g., Mandeville, and at high elevations in the Blue Mountains; Schoener and Schoener, 1971). In allopatric locations, *A. opalinus* is found in the sun rather than the shade

(Underwood and Williams, 1959; Schoener, 1970; Schoener and Schoener, 1971; Jenssen, 1973; L. Fleishman, personal communication). Interestingly, *A. opalinus* prefers low perches unless displaced to higher perches by the occurrence of *A. lineatopus* (Schoener and Schoener, 1971; Jenssen, 1973). Moving higher on tree trunks brings *A. opalinus* into contact with *A. grahami*, which prefers sun to shade. Therefore, it seems possible that light habitat partitioning by *A. grahami* and *A. opalinus* over most of the island may be a consequence of interference competition between these two species. Yet, this conclusion raises the following question: If occupation of shady rather than sunny light habitats by *A. opalinus* is a result of thermal/spatial competition with *A. grahami*, then why has selection not favored dewlap coloration in the former species that is better suited for detection in the shade? We suggest the possibility that *A. opalinus* dewlap coloration may be an evolutionary compromise in an opportunistically heliophilic species. Nevertheless, although observations indicate that *A. opalinus* prefers to perch in the sun when circumstances permit, the opportunity to do so seems to be relatively rare. Clearly, this issue warrants future attention.

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