Interacting effects of canopy geometry and display activity timing shape conditions for visual signalling in Victoria's riflebird

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SUMMARY

Lighting conditions in forests are highly variable in both space and time and depend on the interacting effects of canopy geometry, weather, and the time of day. This has strong implications for visual signalling, because different species sharing the same forest habitat may display in dramatically different microhabitats favouring disparate signal phenotypes. However, relatively little is known about the lighting conditions occurring during visual communication in most animal species. Using hemispherical canopy photography and behavioural data, we investigated lighting conditions of the courtship signal irradiance microhabitat in male Victoria's riflebirds (*Ptiloris victoriae*) — a bird-of-paradise (Aves: Paradisaeidae) endemic to sub-tropical Australia. Despite no detectable differences in crude rainforest canopy features between male display perches and nearby microhabitat control sites, display sites always featured a small gap directly overhead. We then show that males typically display to females in the early morning, especially within the first two hours after civil dawn. Integrating canopy features and display times, we then simulated under-canopy solar irradiance at exact display times and show that males generally display under dim lighting conditions in the absence of direct sunlight. Thus, rather than utilising sun flecks to enhance plumage brightness and colour contrast, male riflebirds prefer to display in dim, diffuse light. These results contrast with findings in some other species in which courting males utilise direct sunlight to enhance visual display efficacy. Instead, some species may be specialised for visual signalling in dim light.

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1. INTRODUCTION

The diversity of animal signalling behaviours is striking and represents a central subject of interest in behavioural ecology. To make sense of this diversity, it is not only important to investigate signal properties, but also conditions of the sensory environment, because effective signalling requires that the signal is emitted under appropriate environmental conditions that maximise transmission and reception [1,2]. However, in any given habitat, physical properties of the environment that influence signal transmission are often highly variable in both space and time [3]. This means that selection cannot fully prepare a given signaller to emit an optimal signal across the full range of sensory contexts it encounters. In forests, for instance, the intensity and composition of light varies dramatically with the angle of the sun, weather, and vegetation structure [3–5]. Moreover, because a species' ecological demands — such as foraging needs or predation avoidance [1,6,7] — shape daily activity patterns, signallers are constrained in both when and where they can display. For instance, some rainforest bird species display early in the morning and late in the afternoon, while others tend to display closer to midday [4]. It is often assumed that birds which display in the forest understorey are subject to dim lighting conditions [8,9], though males of some species actively position themselves inside strongly illuminated sun flecks on the forest floor during display, while others prefer shade [4]. To understand the lighting conditions relevant for visual signal transmission and reception in any given habitat, it is therefore essential to consider both spatial and temporal features of the display microhabitat.

Although there are numerous studies linking animal colouration to general features of their habitats (e.g., [3,10–12]), much less is known about fine-scale microhabitat properties associated with elaborate visual displays in the wild. It is particularly challenging to understand the precise lighting conditions under which visual displays are produced as they are often short-lived and difficult to observe. However, some bird species display from regular display sites and return to these sites at predictable times of the day, suggesting that signallers display under precise local lighting conditions [4,13,14]. For example, Endler (2025) [15] reported fine-scale forest canopy geometry differences between active display sites and random microhabitat sites, as well as abandoned display sites among bowerbird (Aves: Ptilonorhynchidae) species, suggesting that males prefer specific lighting conditions for display. However, it is less well understood how spatial features of the microhabitat interact with daily activity patterns to determine lighting conditions during courtship and how these features are associated with signal transmission and reception. A detailed understanding of these features may not only illuminate the conditions that favour signal transmission, and therefore shed light on the modes of selection that shape signal design, but may also explain why we see such a diversity in complex signals among animals occupying similar habitats [8,9].

The visual display behaviours and ornamental plumage of male birds-of-paradise (Aves: Paradisaeidae) are perhaps the most phenotypically diverse among any single bird family [16,17]. Comparative work shows that some visual signal features are associated with properties of the signalling habitat, suggesting a role for sensory drive [8,9]. However, we currently know very little about the sensory microhabitat of any one bird-of-paradise species, including local lighting conditions during visual displays. To fill this knowledge gap, we investigated specific properties of the signal microhabitat in male Victoria's riflebirds (*Ptiloris victoriae*) — one of four bird-of-paradise species found in Australia (including two other species also found in New Guinea) (**Figure 1A**) [18]. This species is endemic to the Wet Tropics Region, where it inhabits old growth rainforests (**Figure 1B**) [19,20]. Males display from the tops of dead tree stumps in the rainforest understorey and consistently use the same perch repeatedly within breeding seasons [21,22] (**Figure 1A**). Riflebird sexual displays are therefore constrained to a highly specific location, meaning that the visual properties of these displays are likely associated with highly localised lighting conditions. Moreover, since displays occur in a restricted area, riflebirds are a useful system in which to study the light microhabitat, because irradiance can be quantified precisely in space and time.

Figure 1. Complex display behaviour and the signalling environment in Victoria's riflebird. (**A**) Adult males display to females from traditional perches in the rainforest understorey. The *alternate wing-clap* display (shown here) occurs at close range when females visit the display perch [21] (photo taken by TM). (**B**) Riflebirds typically display in old growth rainforests under dense canopy coverage (photo taken in study site by Jack Rees-Elford). Lighting conditions in such forests vary significantly depending on local canopy features and the time of day.

First, we investigated whether riflebird display perches exhibited different patterns of canopy geometry compared to a random sample of control sites surrounding each display perch, as in Endler (2025) [15]). We then incorporated riflebird display activity data to explore how canopy geometry interacts with activity patterns to determine the precise lighting conditions during which females are displayed to by males. By comparing solar irradiance estimates a) between display times and random timepoints at display perches and b) between

display perches and control sites in the immediate surroundings at known display times, we also test whether male riflebirds exhibit features of either temporal or spatial microhabitat use, respectively. Finally, using *in vitro* spectral measurements of feathers sampled from key colour patches used in display, we investigated how the composition of ambient light spectra affects contrast.

2. METHODS

a) Field site, study system, and behavioural recording

Display behaviours of adult male Victoria's riflebirds (*Ptiloris victoriae*) were recorded in rainforest habitats in the Atherton Tablelands in Queensland, Australia (17˚, 15', 55" S, 145˚, 37', 47" E, mean elevation of sampled sites = 753 m) using motion-triggered trail cameras (Browning Recon Force Advantage HD; Browning Recon Force Elite HP5). Cameras were each installed as close as possible to the display perches by mounting them on adjacent trees as perpendicular as possible to the top of the perch. Bird banding was conducted with the approval of the Australian Bird and Bat Banding Scheme (R-class banding authority number: 3662; ABBBS project number: 3662-01). Ethical approval was granted by the Animal Ethics Committee of the Department of Agriculture and Fisheries (AEC reference number: CA 2022/02/1589). Field activities in and around the Crater Lakes National Park (17.283°S, 145.625°E) were each approved by the Queensland Wildlife and Parks Service (P-PTUKI-100257238; WA0045747). Three adult males were banded out of a total of 12 filmed throughout the study and were the only individuals to use their respective display perches within a breeding season, so banding was not necessary for the other perches. Moreover, we confirmed that we did not record the same male at separate display perches through observations of males within their home ranges. Following MacGillavry et al. [23] and Grant and Litchfield [20], we assume that one adult male primarily uses one main display perch within a breeding season.

Male riflebird display perches were located by following advertisement song and validating the frequent use of display perches to ensure it was not an opportunistic display site by continuous monitoring of trail cameras throughout the breeding season (August-November 2022 and 2023). Although male Victoria's riflebirds are known to display opportunistically from numerous perches in their home range, field observations and automated video recordings show that they are extremely loyal to one display perch within a breeding season so long as it is not destroyed by adverse weather or falling vegetation [20,23]. Display behaviours were extracted from camera trap video footage. Male riflebirds produce two common display behaviours — the *circular-wings* display and *alternate wing-clap* display (see [21,23]). The present dataset includes only occurrences of the dynamic *alternate wing-clap* display because

this behaviour occurs only at close range to a receiver; this specifically only includes displays that were directed at conspecifics visiting the display site. Establishing that receivers were female is important because males are known to direct the *circular-wings* display at rival adult males as well as occasionally at heterospecific bird species, but not the alternate wing-clap display [19,21]. Overall, our display dataset therefore specifically includes instances where adult males displayed to female-plumaged receivers that visited the display perch. Although immature males may also visit adult male display perches (MacGillavry, *personal observation*), this is likely uncommon during the breeding season, during which immature male attendance at adult display sites has been shown to decline steeply in species with similar mating systems [24].

b) Hemispheric canopy photos and analysis

Hemispheric photographs were taken using a Canon EOS 5D equipped with a Sigma EXDG 8 mm 1:35 360° solid angle fisheye lens (see [15]) (**Figure 2**). Where possible, hemispheric photos were taken at the top of riflebird display perches using a bubble level to ensure the lens was pointing directly upward. Although 12 adult male perches were monitored in a previous study [23], five of these perches were too unstable to climb safely or were otherwise inaccessible (e.g., too high). All photographs were taken with a compass as a reference so that the top of the image oriented towards magnetic North. We took hemispheric photos of 7 display perches that could be accessed with our camera setup, either because they were low enough to the ground or because they could be safely accessed with a ladder. Although this may introduce some bias in our hemiphoto analyses, perch heights in our sample fall within the typical range of display perch heights seen for this species (mean ± SD = 2.75m ± 0.81, range of all display perches monitored in study site [min - max] = 1.32 – 5.76 m), though shorter perches may still be overrepresented [19]. Nonetheless, all hemispheric photographs were taken at display perches where males were recorded displaying throughout the breeding season. For microhabitat control sites, we took hemispheric photographs (5 – 10 per display site, depending on accessibility) in a 10 m radius surrounding the display perch at random directions using a ~1.8m folding ladder to simulate conditions at common display perch heights. Subsequent processing of hemispheric photos was conducted in MATLAB R2024B [25] following Endler [15].

The blue channel of the coloured hemispheric images was thresholded to black and white using the MATLAB *imbinarize* function with a threshold of 0.6. This estimates the fraction of sky showing through the canopy (i.e., thresholded to white from blue and white pixels). The thresholded image pixels are white for sky and black for vegetation. For each photograph, the entire hemisphere was then divided up into 254 sectors (see **Figure 2**), each in one of 9 annuli (with the first annulus including both the first ring and the centre circle). In each sector, the

gap fraction was calculated from the total number of white (sky) pixels in the sector divided by the total number of pixels (sum of white & black pixels). Note that sectors in the outer annulus are mostly distant ground, dense vegetation, or tree trunks in the horizontal direction and therefore not strictly canopy features.

To quantify differences in canopy structure between display perches and microhabitat controls, we computed the standard deviation (SD) and Hill diversity index (*h*) of sector gap fractions for each hemispherical photo. Gap SD reflects spatial variability within a canopy image. The Hill diversity index was calculated by dividing each sector gap fraction within each image by the sum for all sectors (in that image), yielding proportions summing to 1 for each image. We then calculated *h* from these proportions for each image, which reflects an estimate of the evenness of canopy structure. More precisely, *h* gives an estimate of the number of sectors with similar gap fractions, where larger and smaller values indicate a more variable or more uniform canopy, respectively (see [15] for more information about calculations).

c) Simulating solar irradiance versus time of day

To understand the distribution of male riflebird displays to visiting females across our sampling period, we calculated the hours since civil dawn (the time at which the upper margin of the sun disk is 6˚ below the horizon, corresponding to first light) using the R *lubridate* package [26] and the getSunlightTimes function from the *suncalc* [27]. To simulate direct solar irradiance at known display perches and display times using the hemispherical photographs, we implemented two MATLAB m files written by JAE: GetSuntrackData.m and GetHemiSunTracks.m, where the former calls the latter. These two m files are given in the Supplementary Information.

First, hemispherical photographs were converted to grayscale, by extracting and thresholding the blue channel (see above). This removes bright areas due to sunlit leaves, leaving white and blue for sky. We then used GetHemiSunTracks to model the sun track in a circle with radius of 1 for a given day and location. This outputs the circle, tracks in the circle, times for each point in the track, sun azimuth, and zenith angles for each point, string containing date, and Julian date. We then used methods in the WINPHOT software manual [28] and Meeus [29] to calculate photosynthetically active radiation (PAR) above the canopy using output values of GetHemiSunTracks for each point and time in the solar tack. Sun tracks were then rescaled with corresponding PAR to match the outline of the hemispherical photograph allowing us to overlay the sun tracks onto the hemispherical photograph. We then calculated the fraction of the sun disk showing through the canopy at each calculated time point on the sun track. Following this, we multiplied the fraction canopy for a given time by the PAR above canopy to estimate the PAR as a function of time below the canopy. Because this does not account for light scattering from vegetation and clouds, and refraction of light around

the earth's atmosphere before the sun disk intersects the horizon, we added 0.0004 to irradiance values of 0 to account for diffuse light based on crepuscular forest light data published in Endler (1993) [3].

We then investigated a) temporal light microhabitat usage and b) spatial microhabitat use. To test for temporal light microhabitat usage, we calculated solar irradiances at display perches at random timepoints in the daily light curve for each given display ('RdIrrad') to compare with observed solar irradiances at known display times. This yielded a sample of n = 431 display irradiance values and n = 431 random irradiance values. To test for spatial light microhabitat use, we calculated solar irradiance values at exact display times for each display for each microhabitat control site photographed at each display perch. This yielded a sample of n = 3495 control solar irradiance values corresponding to the 5-10 microhabitat control hemiphotos taken for each of the 7 display perches and 431 recorded displays. We then compared perches to controls for all statistics.

d) Statistical analysis

To investigate differences in canopy gap statistics, we fit a series of models using a linear mixed model (LMM) with the *lme4* [30] and *lmerTest* [31] packages in R version 4.4.2 (2024-10-31) [32]. We set gap fraction as a response term, site (microhabitat control or display perch) as a categorical predictor, and perch number as a random intercept term. We then fit a null model including only an intercept and no fixed predictors and compared the fit of this model to the full model ("full-null" model comparison) using a log-likelihood ratio test (ANOVA function, test = "chisq") [33]. Diagnostics were performed with the *DHARMa* package [34]. We inspected the normality of residuals and tested for overdispersion using the KS test and then examined model stability by excluding each level of the random effect at a time and comparing the estimates derived from these models to that of the full model [35]. The effects of all models were stable.

Visual inspection of hemiphotos suggested that display perches exhibit a small gap directly overhead. To test this statistically, we fit a Generalized Additive Mixed Model (GAMM) with packages *mgcv* 1.9–3 [36] and *itsadug* 2.4.1 [37] following Endler (2025) [15], as this allows for nonlinear associations between sector brightness and annulus number. This model included sector brightness as a response term, annulus number (continuous model term) as a fixed predictor and annulus number as well as site (display perch or microhabitat control) as smooth terms, and perch ID as a random effect to account for the inclusion of multiple replicate control sites per display site. Results were then plotted using the *ggeffects* package [38]. See **Table 1** for full model results and **Figure 3A** for plotted effects.

Because observed irradiance values were heavily skewed towards zero with a long right-tail, we compared temporal and spatial light microhabitat irradiance values using a zero-

inflated GLMM. We first selected the appropriate error distribution by inspecting Cullen & Frey graphs (see **Figures S1** and **S2**) made using the *fitdistrplus* 1.2-6 package [39]. Following this, we fitted zero-inflated GLMM models with a Gamma error distribution in the *glmmTMB* 1.1.11 package [40]. To test for temporal microhabitat use, we then included actual versus randomly sampled irradiance times (irradiance times at random time points in the light curve of the specific date during which a given display occurred) as a fixed model term and display perch ID as a random effect (model a). For spatial microhabitat use, we included location (microhabitat control versus display perch) as a fixed term and display perch ID as well hemiphoto image ID as random effects as there were replicates within display perch ID and each hemiphoto (model b). Diagnostics were performed as described above. Residuals in both models differed significantly from normality (KS test $p > 0.05$) and model a violated the homogeneity of variance assumption (Levene test in the *DHARMa* package). We thus urge some caution in interpreting the outputs of these results and note that GLMMs are generally robust to deviations from normality of residuals [41]. To provide more support for our results, we re-ran models with a Tweedy distribution using the *glmmTMB* package, which also accounts for high zero counts in the datal model results were similar to those of the zero-inflated models, see **Table S1**.

e) Feather sampling and colour analysis

Feather spectra were collected for another study by Carboon et al. (*forthcoming*), which measured angle-dependent spectra of individual feathers using a goniometer following Ospina-Rozo et al. [42]. This is important for riflebird plumage as feathers on the blue-green gorget appear highly specular [43]. For colour analyses, we used maximal reflectance (radiance) values for each sampled feather, taken from a) the 'Gorget' (blue-green throat patch), b) the 'Breast' (glossy green abdominal feathers), and 'Dark' chest patch (a super-black patch on chest between the Gorget and Breast patch). Because only $n = 2$ specimens were sampled, we selected the specimen with the highest quality spectra for further analysis.

To estimate colour contrast Colour and luminance contrast among colour patches, we then calculated ΔS based on the Receptor Noise Limited model of Vorobyev and Osorio (1998) [44] assuming a violet sensitive type eye for birds-of-paradise based on Endler and Mielke (2005) [45] and Ödeen et al. (2011) [46]. We applied von Kries corrections for sidewelling light using an intermediate noise estimate ($nu = 0.3$), as this is most ecologically relevant for riflebirds, where displays are viewed horizontally and most light comes from directly above the male. To test the hypothesis that male colouration is more conspicuous under display lighting conditions, we calculated ΔS between pairs of colour patches given the five main forest light environments in Endler (1993) [3]: early/late, forest shade, woodland

shade, open/cloudy, and small gaps. Due to our small sample of individuals, these analyses should be considered preliminary.

3. RESULTS

a) Canopy geometry

The GAMM annulus test shows that sector gap fraction increases towards the zenith (centre of the hemiphoto or the first annulus), where the annulus above display perches was much brighter than in microhabitat control sites (**Figure 2A**-**C**, see **Table 1**). Although there was evidence of a canopy gap directly above display perches, we did not detect any differences in general gap metrics between display perches and control sites (**Figure 2B**). For instance, there was no significant difference in total gap fraction between microhabitat control sites and display perches (full-null model comparison [LMM], χ^2 = 1.290, p = 0.256) (**Figure 3B**) and there was 99% overlap between hulls (relative to the smaller hull) in a bivariate plot of gap SD versus gap Hill diversity (**Figure 3C**). We note, however, that our sample size was relatively small and asymmetrical (more controls than perches), so it is possible that a larger sample size will reveal a significantly larger gap fraction for display perches since they are brighter directly overhead. Nonetheless, this effect was small enough that we could not detect in in our sample, suggesting that overall differences between display perches and local microhabitat controls are minimal. Indeed, **Figures 2D** and **2E** show that there is no obvious pattern differentiating general canopy features between display perches and microhabitat controls, despite display perches exhibiting a small gap directly overhead.

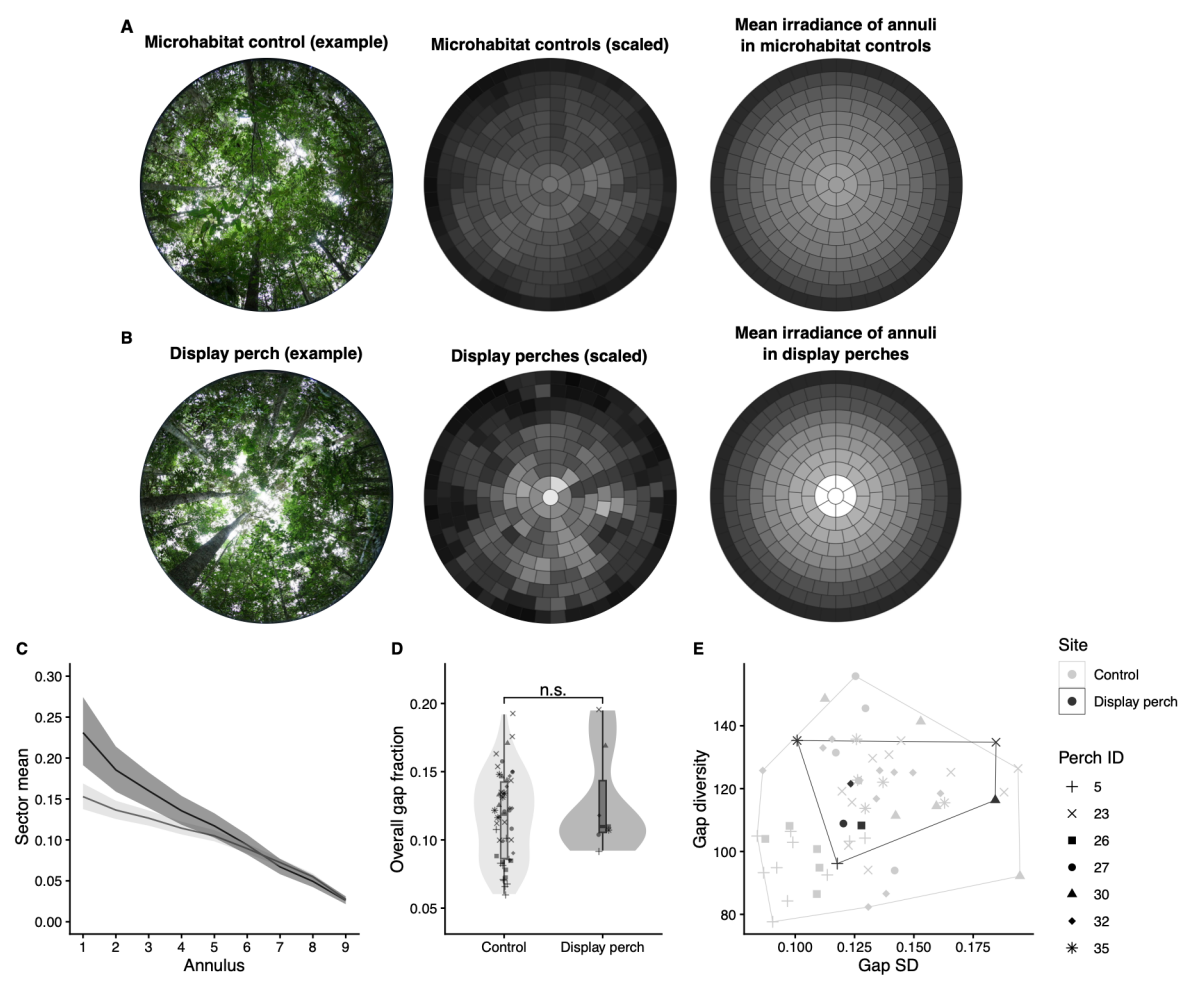

Figure 2. Differences in canopy structure features between display perches and microhabitat control sites. Hemiphotos taken from a sample of microhabitat control sites (**A**) and riflebird display perches (**B**) (see Methods) show a gap directly overhead for display perches. In **A** and **B**, an example hemiphoto for each condition, averaged gap fractions for each sector (where brightness indicates higher mean sector openness), and averaged values within hemiphoto annuli are shown. (**C**) Predicted effects from a GAMM testing the effect of annulus number (1 to 9 corresponding to central to peripheral annuli, respectively) and site (microhabitat control or display perch) on annulus mean gap fraction (modelled with perch ID as a random term) (see **Table 1** for model output). The dark and light grey lines represent display perches and microhabitat control sites, respectively. Lines denote model effects and shaded regions show 95% confidence intervals. Display perches are brighter in the central annulus compared to microhabitat controls. (**D**) Total canopy coverage (hemispheric gap fraction) does not differ between display perches and microhabitat control sites. Boxes inside violin plots show medians, upper and lower quartiles, and the interquartile range. (**E**) Sector gap fraction Hill diversity (*h*) plotted against sector gap fraction SD for display sites and microhabitat control sites. Dataset includes N = 7 active display perches and N = 50 controls (5 – 10 per display perch).

Table 1. Results of GAMM comparing sector gap fractions across annuli between display perches and microhabitat control sites. See visualisation of predicted effects in **Figure 2C**. SE = standard error, edf = estimated degrees of freedom, Ref.df = reference degrees of freedom.

Parametric coefficients				
Term	**Estimate**	**SE**	**t-value**	**p-value**
(Intercept)	0.552	0.043	12.72	**< 0.001**
Annulus	-0.034	0.006	-5.69	**< 0.001**
Approximate significance of smooth terms				
Term	**edf**	**Ref.df**	**F**	**p-value**
s(Annulus, Site)	12.009	16	14.45	**< 0.001**
s(Perch)	5.969	6	153.96	**< 0.001**

b) Activity patterns and display lighting

Trail camera recordings show that males displayed predominantly in the early morning, with a significant peak within the first two hours after civil dawn, though some increase in activity was recorded in the late afternoon (**Figure 3A**). Nearly a third (27.2%, n = 120) of displays occurred within the first hour after civil dawn and about half (49.0%, n = 215) within the first two hours, with a second, smaller peak of activity in the evening ~10 hours after civil dawn (between 4-6 pm). Solar irradiance values simulated using hemispheric canopy photographs at each known display time show that displays predominantly occurred in the absence of direct solar illumination, usually under dim lighting, meaning that male riflebird displays occur at locations and times of day during which virtually no direct sunlight reaches the display site (**Figure 3B**). This result needs to be interpreted with caution, as it does not account for diffuse lighting, especially given the small canopy gap directly overhead. Considering only the above-canopy light which would be important on cloudy days [3] also shows that riflebird displays tend to occur when illumination is extremely low (**Figure 3C**). The distribution of solar irradiance values is skewed towards zero when canopy geometry is included, meaning that light conditions during display arise from an interaction between canopy geometry and display timing (**Figure 3B**).

Comparing solar irradiances at exact display times to a random sample of irradiance values taken from random times in the daily light curve within which each given display occurred shows that displays tended to occur during dimmer illumination than random (full-null model comparison [zero-inflated GLMM; family = Gamma], $\chi^2 = 27.525$, p = < 0.001; see **Table 2**). In contrast, no significant difference between display perch lighting and lighting at microhabitat controls at the exact times of display was detected (full-null model comparison [zero-inflated GLMM; family = Gamma], $\chi^2 = 1.030$, p = 0.310). These results indicate that the occurrence of display in the early/late light microhabitat is the defining characteristic of sensory microhabitat use in male Victoria's riflebirds, whereas we did not find evidence for fine-scale

differences in spatial microhabitat use beyond the general pattern that riflebirds generally display in the middle strata of rainforest below the canopy.

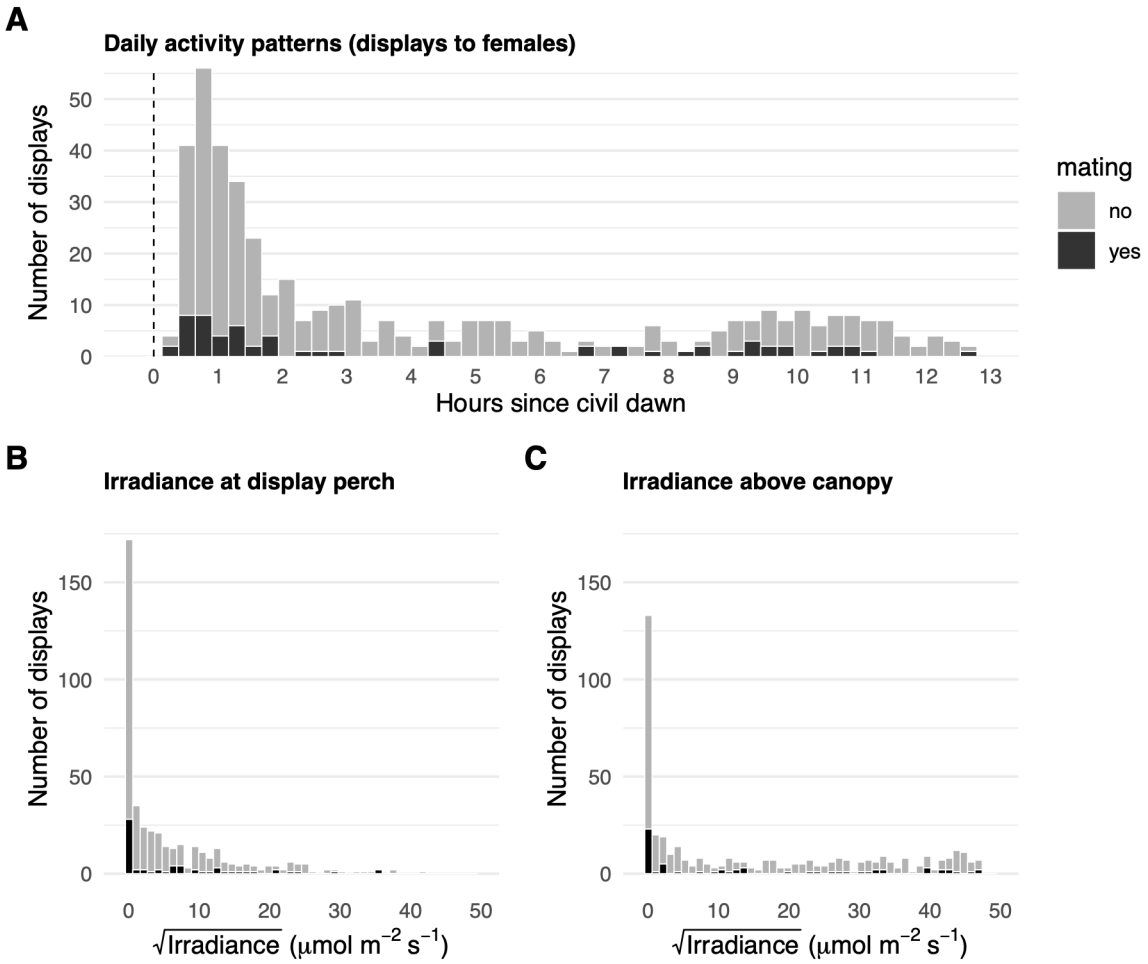

Figure 3. (**A**) Distribution of display times (stacked bar plot) relative to civil dawn (defined as when the sun is 6˚ below the horizon, associated with first light) (n = 431 displays, n = 7 adult males). (**B**) Simulated solar irradiances (PAR) at display perches at known display times shows a strong concentration of display at ~0 irradiance, suggesting that males are preferentially visited by females under low direct illumination. Because light is refracted around earth's atmosphere before the solar disk crosses the horizon, but the hemisphere canopy data does not account for this, we converted zeroes to 0.00004 based on measurements of solar illumination in early/late conditions based on Endler (1993) [3]. (**C**) Simulated PAR at known display times above the canopy. Note that the distribution in C is much more uniform than B despite both showing peaks at ~0 irradiance, suggesting males preferentially display out of direct sunlight. In **B** and **C**, we show the square root of irradiance for visualisation.

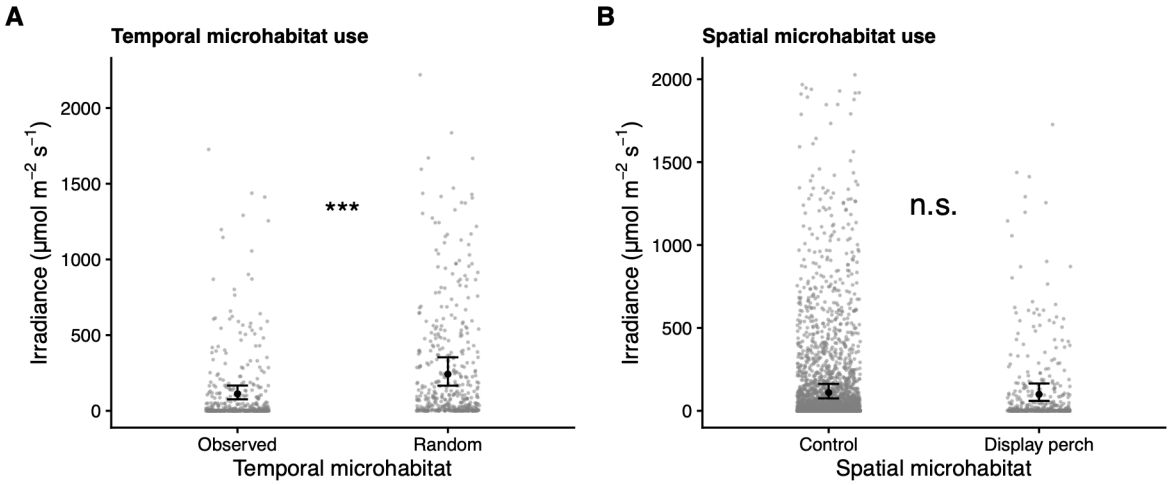

Figure 4. Evidence of temporal (**A**) but not spatial (**B**) microhabitat selection in courting Victoria's riflebirds. (**A**) Simulated irradiance levels during exact times at which males display to receivers ('Irrad') are significantly lower (i.e., darker) than irradiance levels sampled from random times in the daily light curve ('RdIrrad') for each given display. (**B**) Solar irradiance levels did not differ between spatial microhabitat controls ('control') sampled within a 10m radius around each display perch (see **Methods**) and the display perches themselves ('display perch') at exact times of display. In panel **A**, each point represents a display (n = 431 displays in each level of the x-axis) , whereas in panel **B** there are more data points for 'control' as we sampled 5-10 spatial microhabitat controls for each display perch (see **Methods** for more information).

Table 2. Results of zero-inflation GLMMs with a gamma error distribution testing for difference in temporal and spatial microhabitat usage accounting for zero-inflation in solar irradiance. Both models account for individual variation by including male ID as a random effect. The model investigating spatial microhabitat use also includes photo ID as a random term. Similar results are obtained when re-fitting models using a Tweedy distribution (**Table S1**).

Model	Coefficient	Estimate	Lower CI	Upper CI	SE	z	P
Temporal microhabitat use	(Intercept)	4.723	4.329	5.117	0.201	23.488	**< 0.001**
	type: Random	0.767	0.486	1.047	0.143	5.357	**< 0.001**
Spatial microhabitat use	(Intercept)	4.742	4.353	5.132	0.199	23.859	**< 0.001**
	display: Display perch	-0.124	-0.359	0.111	0.120	-1.031	0.302

c) Contrast and receptor stimulation

Colour contrast between colour patches was consistently highest in the early/late microhabitat, though only marginally so, whereas double cone and rod (luminance) contrasts were not consistently highest in any one light microhabitat (see **Table 3**). Luminance contrast was highest between the dark chest patch ('Dark') and specular blue-green gorget ('Gorget'). Most importantly, colour and luminance contrast were never highest in the open-cloudy microhabitat, which is virtually never used by adult male riflebirds during the breeding season.

Table 3. Measures of chromatic and luminance contrast (ΔS from Vorobyev and Osorio 1998) among colour patches and compared to the background. A value of 1 represents a just noticeable difference. Note that colour (single cone) contrasts tend to be higher in the EL habitat than others, although differences are generally small. Differences among light environments are generally small because spectral shape and light captures varied substantially among patches (see **Table S2**). Bold numbering indicates the highest values for a respective pair. Light habitats are FS = forest shade, WS = woodland shade, SG = small gaps, OC = open/cloud, and EL = early/late as in Endler (1993) [3].

SINGLE CONE CONTRASTS (colour) nu=0.3					
Pairs	**FS**	**WS**	**SG**	**OC**	**EL**
Breast-Dark*	2.904566	2.919307	2.89611	2.913771	**2.943216**
Breast-Gorget*	6.790899	6.752859	7.010117	6.917714	**7.173199**
Dark-Gorget*	4.741372	4.703432	4.899934	4.831084	**5.031464**
DOUBLE CONE CONTRASTS (luminance)					
Pairs	**FS**	**WS**	**SG**	**OC**	**EL**
Breast-Dark*	20.459322	20.41727	**20.597129**	20.509998	20.503179
Breast-Gorget*	18.965573	**19.017862**	18.550019	18.79023	18.783958
Dark-Gorget*	39.424895	**39.435131**	39.147148	39.300228	39.287137
ROD CONTRASTS (luminance)					
Pairs	**FS**	**WS**	**SG**	**OC**	**EL**
Breast-Dark*	19.271976	19.15923	**19.389702**	19.295929	19.274882
Breast-Gorget*	**20.007047**	19.835521	19.969875	19.915059	19.803606
Dark-Gorget*	39.279024	38.994751	**39.359578**	39.210988	39.078488

4. DISCUSSION

Visual signals are generally adapted to maximise their transmission and reception under the typical light conditions during which they are produced [1,5,47–52]. However, because light conditions are highly variable in both space and time, a detailed understanding of the conditions during signal production is required to make sense of animal colour patterns and visual signal design [3,15,51,53]. In forests, lighting conditions that affect signal transmission and reception vary as a function of several features, including vegetation structure, sun angle, weather, and their interaction [3]. As a consequence, animals may prefer to display in specific, local sensory microhabitats that exhibit specific optical properties, as this provides consistent conditions for signal transmission and reception [4,4,15,53]. By integrating canopy geometry, display activity, and estimates of solar irradiance during sexual display in Victoria's riflebird, our study illustrates how the interaction between behaviour and the physical environment shape lighting conditions during sexual signalling, emphasising the central importance of display timing in taking advantage of light conditions.

a) Solar geometry, activity patterns, and light conditions during display

We found that the geometry of vegetation above the display perches of male Victoria's riflebirds differs in specific ways from a random sample of locations surrounding the display

site. Although we did not detect differences in general canopy features, display perches consistently had a small canopy gap directly overhead (see **Figure 2**). Such a canopy gap may improve the intensity and contrast of the structural blue-green throat patch, which reflects strongly in a few directions (see **Figure 5**). Males point their head upwards during display (see [23], which may reflect a large portion of downwelling diffuse light directly at the females' eyes because the angles between irradiance, feather angles, and female position is aligned with the maximum reflectance angle (see **Figure 5**). Because these canopy gaps were relatively small, the effect may not be large, especially when the sun angle is low (as for most displays), but even at low sun angles more light comes from above in the forest because there is more vegetation horizontally than vertically.

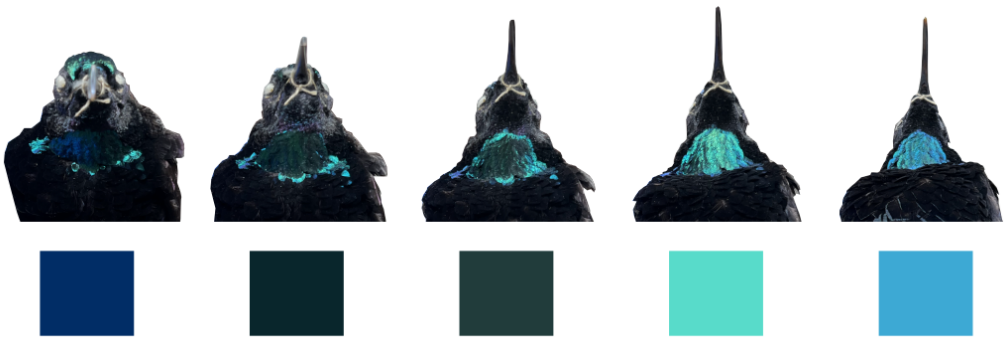

Figure 5. Photographs showing the specular nuptial gorget of male riflebirds. The bird skin shown here is a Paradise riflebird (*P. paradiseus*), which is extremely similar to Victoria's riflebird in plumage and display behaviour and is used only for illustrative purposes here. Squares show pixel values of the central point on the gorget for illustrative purposes.

A canopy gap directly overhead may be an incidental byproduct of the fact that males tend to display on tree stumps. A tree stump is beneath the former canopy of the missing part of the tree, and this canopy reduction or gap should therefore shape lighting conditions during signal production on the stump. Such incidental features of the display microhabitat are relevant to signal evolution as they may correspond with features relevant for signalling, although it is unclear whether they are actively selected by males. In some species, for instance, signallers select optimal display sites and actively position themselves in local lighting conditions that maximise signal transmission during display [4,14,15,54]. In others, signallers specifically orient themselves relative to the sun to control specific features of the visual display, often with clear effects on conspicuousness [4,54–57]. Some birds are also known to behaviourally modify properties of their environment to construct optimal conditions for visual signalling [14,51,58,59]. Other examples of sensory microhabitat choice include the choice of substrates for optimal camouflage [60,61], which in some instances can be improved through experience [62]. However, because our control sites included only a random sample of forest adjacent to display sites and did not include other unused or abandoned perches (the

latter being extremely difficult to find) [15], we lack the data to definitively test whether male riflebirds actively choose display sites based on local canopy conditions. Simulations of solar irradiance further clarify the lighting conditions under which male riflebirds display.

Male riflebirds display to females predominantly in the early morning and less so in the late afternoon (**Figure 3A**). The peak of activity in display behaviour in the first two hours after civil dawn is interesting for several reasons. For instance, for species displaying to receivers early in the morning, most direct solar irradiance is obstructed by canopy vegetation or filtered by leaves. Consequently, the majority of displays occur during low or no direct solar illumination (**Figure 3B, C**), particularly in the dimly lit early morning. Because the sun angle is very low at that time, riflebird displays receive typically receive no direct sunlight. This contrasts with some other rainforest-displaying species that actively position themselves in or across sun flecks under clear sky (i.e., direct sunlight) [4] and has numerous implications for how male displays are perceived by females.

Although many species appear to favour direct sunlight during display [51,54–56,63], it is very unusual to observe adult male riflebirds displaying in direct sunlight other than during "practice" displays from unusually exposed perches outside of the breeding season. Interestingly, the yellow epithelium of the mouth in Victoria's riflebird is theoretically the most intense when perceived under direct sunlight, though it is possible that its primary function is to maximise colour contrast with the blue-green gorget. However, despite the predominance of displays in dim solar illumination, there is variation in light conditions based on simulated irradiance patterns (**Figure 3C**). Despite this range of possible lighting conditions, male riflebirds may generally maintain high chromatic and luminance contrast as colour patches are viewed up close against extremely black plumage (see [23,64] and dark tree trunks. However, although there are some displays with relatively high solar irradiance, we could not account for cloud coverage in our simulations. Based on observations in the field and recorded video footage, it is most likely that these displays occurred under overcast conditions.

b) Implications for visual signal design

The composition of light in forests is mostly purplish-white in the early morning, with a reduction in middle wavelengths, meaning that species displaying under these conditions are predicted to use mostly UV, violet, blue, red, or purple, with some yellow, yellow-green, or green (see [3]. This may help explain why riflebirds incorporate blue-green and yellow colour patches in display, though we could not obtain spectral measurements of the yellow mouth integument. Nonetheless, we find that colour contrast (but not luminance contrast) is consistently highest among three colour patches used during display during early/late light conditions (**Table 3**). Although differences were small, this may still confer a selective advantage during courtship because even a small and within-generation undetectable

selective advantage will spread through a population [65]. Although luminance contrast was not highest under early/late, it was never highest in open/cloudy conditions.

Although colour patch contrast differences were small among light microhabitats, there are other explanations for early/late display efficacy. Peak luminance sensitivities of vertebrate eyes shift towards the peak spectral sensitivity of rods (~500 nm) in low light in a phenomenon known as the Purkinje shift [66,67]. This means that blue-green objects are likely to be perceived as brighter than red objects during dim illumination. During mesopic conditions (dim illumination) at dawn during which riflebirds typically display, blue-green patches could thus appear more conspicuous relative to red ones, suggesting that male riflebird plumage may be tuned to appear relatively brighter under dim light in the early morning. More generally, we predict that blue-green colour patches are therefore more common in visual signals species that display during dim, mesopic conditions ([3], but see [68]. In contrast, species with orange/red patches are expected to display in forest sun flecks or in the canopy, where light is also richer in longer (redder) wavelengths, aligning with previous work on some cotinga and manakin species [3,4]. This pattern is also anecdotally seen in the birds-of-paradise: all species in the genus *Paradisaea* display above the canopy and primarily have orange, brown, or green colour patches, except the blue bird-of-paradise (*P. rudolphi*), which is mainly blue, black, and white, and displays in the understorey [17,19]. Although anecdotal, there are other bird-of-paradise clades that also display under early/late conditions in the understorey, two of which, the sicklebills (genus *Epimachus*) and lophorinas (genus *Lophorina*), convergently evolved blue or blue-green specular patches.

Finally, what we have not considered is that, because riflebirds have much smaller eyes than humans, all else being equal, the dimly lit early morning will appear even darker due to limitations in light-gathering ability of small eyes [69]. However, light gathering of the eye is also influenced by photoreceptor morphology and the transmission of ocular media [70]. Unfortunately, detailed morphological measurements of riflebird eyes are not currently available. Based on measurements of light-gathering ability in other bird species (measured as the ratio of the corneal versus transverse diameter of the eye) suggests a value of 45 and 50 for riflebirds, which is relatively good for passerines, which tend to have small eyes (and small bodies) [71]. It would be interesting to further investigate the visual system of riflebirds to better understand signal perception in this species. This further underscores the importance for future work on signal microhabitats to consider interacting effects of light conditions during signalling, signal properties, and the visual system.

5. CONCLUSION

To conclude, our study illuminates fine-scale spatiotemporal features of the light microhabitat in a poorly known bird species and showcases the central role of behaviour in shaping signal

conditions during sexual display. Without incorporating diel activity patterns at display sites and canopy features, the precise lighting conditions associated with signal production remain unclear. Although it is assumed that the forest understorey is dimly lit [8,9,68], depending on local canopy features, the time of day, and local weather conditions, the forest floor can also contain regions with high solar irradiance (i.e., sun flecks) [3,4]. Because both illumination as well as the composition of light at these locations is highly different compared to forest shade selection may favour highly divergent signal phenotypes within the same habitats. For example, a male displaying on the forest floor will appear highly different if he displays in shade or inside a sun fleck [4]. This may help explain why there is such an extreme diversity in visual signal phenotypes among rainforest-dwelling birds [3,15,72,73], despite occupying the same habitat. This diversity may in part be explained by variation in signalling microhabitats, both in space as well as specific times of display [4,15,52]. More work is needed across different species sharing similar habitats to better understand the diversity of signalling microhabitats and their association with signal design and mating outcomes.

Overall, future research on the interaction between signal properties and forest light requires a better integration of vision — including retinal physiology and eye optics — as well as detailed measurements of light microhabitats, specifically at the exact times when signals are produced.

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SUPPLEMENTARY INFORMATION

Interacting effects of canopy geometry and display activity shape conditions for visual signalling in Victoria's riflebird

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Table S1. Results of zero-inflation GLMMs with a Tweedy distribution testing for difference in temporal and spatial microhabitat usage accounting for zero-inflation in solar irradiance. Both models account for individual variation by including male ID as a random effect. The model investigating spatial microhabitat use also includes photo ID as a random term.

Model	Coefficient	Estimate	Lower CI	Upper CI	SE	z	P
Temporal microhabitat use	(Intercept)	4.428	4.041	4.814	0.197	22.450	**< 0.001**
	type: Random	0.993	0.743	1.244	0.128	7.780	**< 0.001**
Spatial microhabitat use	(Intercept)	4.309	3.775	4.843	0.272	15.824	**< 0.001**
	display: Display perch	-0.045	-0.435	0.344	0.199	-0.228	0.82

Table S2. Delta contrasts (ΔS) with higher noise (nu = 0.5).

SINGLE CONE CONTRASTS (colour) nu=0.5

Pairs	FS	WS	SG	OC	EL
Breast-Dark	1.74274	1.751584	1.737666	1.748263	1.765929
Breast-Gorget	4.074539	4.051715	4.20607	4.150629	4.30392
Dark-Gorget	2.844823	2.822059	2.93996	2.89865	3.018879

DOUBLE CONE CONTRASTS (luminance)

Pairs	FS	WS	SG	OC	EL
Breast-Dark	12.275593	12.250362	12.358277	12.305999	12.301908
Breast-Gorget	11.379344	11.410717	11.130012	11.274138	11.270375
Dark-Gorget	23.654937	23.661079	23.488289	23.580137	23.572282

ROD CONTRASTS (luminance)

Pairs	FS	WS	SG	OC	EL
Breast-Dark	11.563186	11.495538	11.633821	11.577558	11.564929
Breast-Gorget	12.004228	11.901312	11.981925	11.949035	11.882164
Dark-Gorget	23.567414	23.396851	23.615747	23.526593	23.447093

880

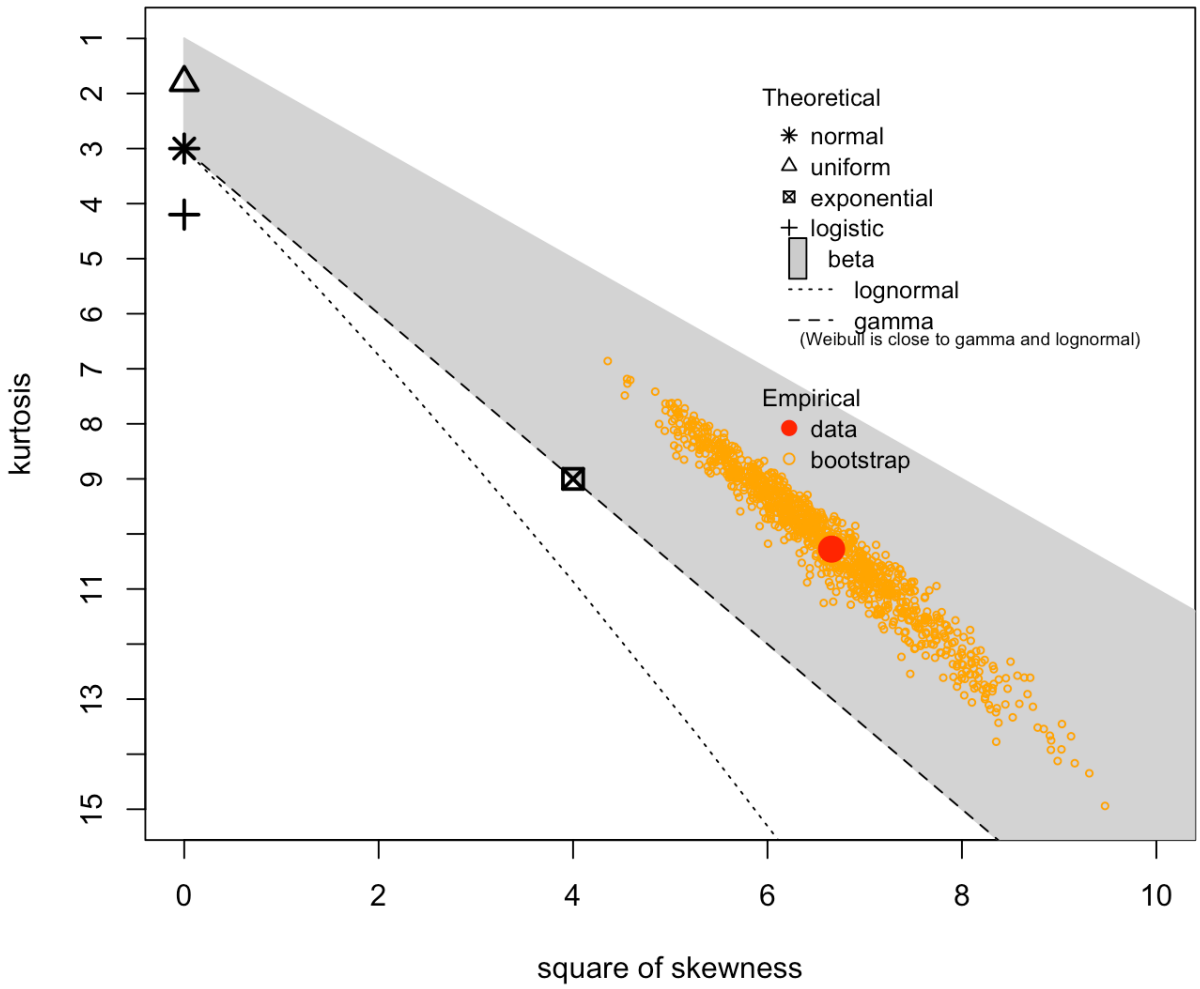

Figure S1. Cullen and Frey graph illustrating the distribution of irradiance values in the temporal control dataset.

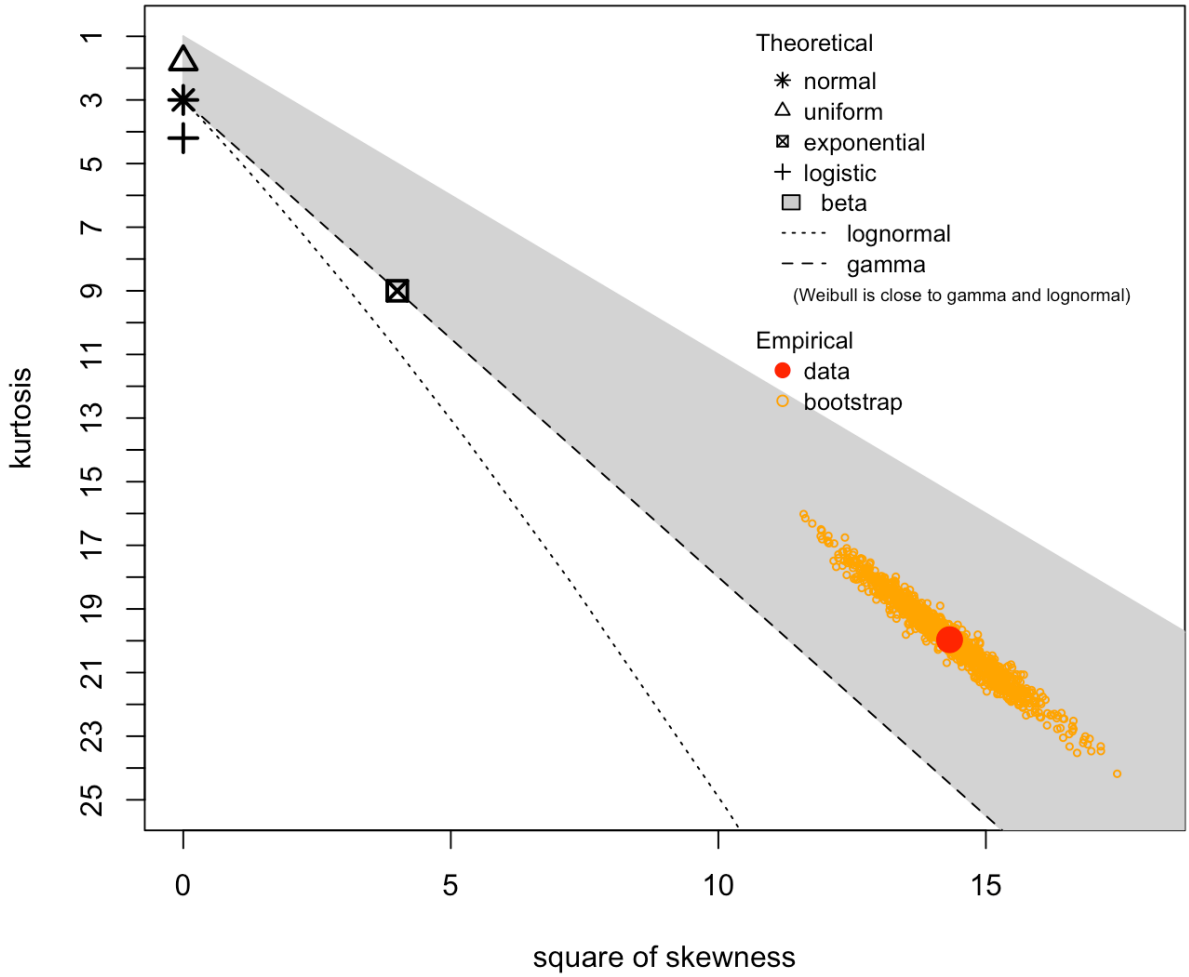

Figure S2. Cullen and Frey graph illustrating the distribution of irradiance values in the spatial control dataset.

890