1 **Flies improve the salience of iridescent sexual signals by orienting**

2 **toward the sun**

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18 **Abstract**

19 Sunlight is the ultimate source of most visual signals. Theory predicts strong selection for its

20 effective use during communication, with functional links between signal designs and display

21 behaviours a likely result. This is particularly true for iridescent structural colours, whose

22 moment-to-moment appearance bears a heightened sensitivity to the position of signallers,

23 receivers, and the sun. Here we experimentally tested this prediction using *Lispe cana*, a muscid

24 fly in which males present their structurally coloured faces and wings to females during ground-

25 based sexual displays. In field-based assays we found that males actively bias the orientation of

26 their displays toward the solar azimuth under conditions of full sunlight and do so across the

27 entire day. This bias breaks down, however, when the sun is naturally concealed by heavy cloud

28 or experimentally obscured. Our modelling of the appearance of male signals revealed clear

29 benefits for the salience of male ornaments, with a roughly four-fold increase in subjective

30 luminance achievable through accurate display orientation. These findings offer fine-scale,

31 causal evidence for the active control of sexual displays to enhance the appearance of iridescent

32 signals. More broadly, they speak to predicted coevolution between dynamic signal designs and

33 presentation behaviours, and support arguments for a richer appreciation of the fluidity of visual

34 communication.

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Introduction

The structure of any effective communication system is shaped its response to basic challenges. Encoding information (Weaver et al. 2018; White 2020), ensuring its delivery (Endler and Thery 1996), and separating signal from noise (Warrant 2016) are essential features of signalling systems, and selection has generated diverse solutions. In general terms, theory predicts the coevolution of signals and signalling behaviours that secure the exchange of information between interested parties while minimising exposure to eavesdroppers (Endler 1992; Endler 1993). Males of the common eggfly *Hypolimnas bolina*, for example, combine limited-view iridescent colours with precision display behaviours to deliver maximally conspicuous signals during courtship (White et al. 2015). Great bowerbirds, by contrast, present coloured objects to females from within constructed viewing 'theatres', and in doing so control both the object of display and the broader visual environment (Endler et al. 2010; Kelley and Endler 2012).

Sunlight is the ultimate source of most visual signals, as its colour and intensity shape the appearance of reflective surfaces. Selection for its effective use should therefore be intense (Endler 1992; 1993). This is particularly true for signal designs whose moment-to-moment appearance bears a heightened sensitivity to local conditions, such as structural colours (Kinoshita 2008; Mouchet and Vukusic 2018). Structural colours result from the selective reflectance of light by tissues organised at the nanoscale and can achieve levels of brightness and chromaticity that are unattainable with pigments alone (Kinoshita 2008; Johnsen 2012). Where coherent or quasi-coherent scattering is involved, as is most often the case, they are also capable of iridescence and limited-view expression (Prum 2006; Vukusic 2006).

60   Given that the optimal colour and/or brightness of iridescent signals is tied to the

61   geometry of the signaller, viewer, and illuminant, its widespread use in nature suggests the

62   existence of flexible behaviours for their effective presentation. That is, signallers should seek to

63   capture available sunlight so as to maximise the conspicuousness of structurally coloured signals

64   to viewers (Endler 1992; Endler and Thery 1996). This prediction has found broad support

65   across model vertebrates with observational evidence showing how signallers vary the timing,

66   location, or orientation of their displays to improve communication efficacy (Endler 1991;

67   Endler and Thery 1996; Dakin and Montgomerie 2009; Bortolotti et al. 2011; Sicsu et al. 2013;

68   Klomp et al. 2017; Simpson and McGraw 2018; O'Neill et al. 2019). Though this work is

69   extremely valuable, a richer causal understanding awaits manipulative tests across temporal and

70   taxonomic contexts.

71   Flies rank among the most diverse animal orders and this is reflected in the traits that

72   have evolved in the service of visual communication (Marshall 2012). Sexually- and

73   ecologically- specialised eye structures (Zeil 1983; Hardie 1986), elaborate colour patterns

74   (Shevtsova et al. 2011; Butterworth et al. 2020), and ritualised display behaviours (Land 1993;

75   Zimmer et al. 2003; Lunau et al. 2006; Butterworth et al. 2019) abound, and offer tractable but

76   underutilised opportunities for general tests of theory. Work on visual signalling in the group

77   continues to document the widespread presence of conspicuous structural colours, with recent

78   efforts highlighting 'wing interference patterns' (WIPs) as potential vectors of information

79   (Shevtsova et al. 2011; Katayama et al. 2014; Hawkes et al. 2019; Butterworth et al. 2020).

80   These striking patterns are the result of thin film interference from chitin/air interfaces in the

81   wing membrane (Shevtsova et al. 2011) and they are regularly presented during courtship (Land

82   1993; Frantsevich and Gorb 2006; Katayama et al. 2014; White et al. 2020). The wings bearing

83   them are also typically transparent and transmit ca. 70-80% of incident light. This combination

84   of iridescence and transparency makes their appearance uniquely environmentally contingent

85   since bright visual backgrounds or the misalignment of signallers, receivers, and the sun will

86   render the patterns invisible. The significance of visual backgrounds during signalling is well

87   demonstrated (Katayama et al. 2014) and includes evidence for active choice in the wild (White

88   et al. 2020). Whether and how signallers actively use the sun to improve communication,

89   however, is unknown.

90   The genus *Lispe* is a cursorial group of muscid flies comprised of at least 163 species

91   spanning most terrestrial biogeographic regions (Pont 2019). The group showcases striking

92   interspecific and sexual variation in colouration and displays (Frantsevich and Gorb 2006; Pont

93   2019). *Lispe cana* is an exemplar endemic to the foreshores of Australia's east coast. Males and

94   females of the species bear structurally coloured UV-white and yellow faces, respectively, as

95   well as dimorphic wing interference patterns (unpublished data). During their ground-based

96   courtship male *Lispe cana* approach and straddle females from behind and maintain this position

97   as females walk about the environment. They then release and move directly in front of females

98   to present their faces and wings in a ritualised 'dance' (White et al. 2020). Males can and do

99   enhance the salience of their signals through the selection of backgrounds against which to

100   display, and similar potential benefits exist through the careful use of sunlight.

101   Here we use observational and manipulative field-based assays at a fine temporal scale to

102   test the hypothesis that males should orient their displays toward the sun so to improve the

103   salience (and, hence, attractiveness) of their iridescent signals. This predicts a bias in the

104   orientation of male displays toward the sun's azimuth position under clear skies, when the its

105   position is readily visible and the potential benefits for signal salience are likely maximised. As a

106   corollary, the natural or artificial removal of direct sunlight should disrupt any orientation bias

107   by either impeding male's ability to orient and/or diminishing the benefits of such behaviour for

108   the salience of signals.

Methods

109

Sexual displays and orientations

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111   Courtship in *Lispe cana* proceeds in four general stages: (1) males detect females when

112   both parties are walking about their foreshore habitats; (2) males approach females from behind,

113   before 'straddling' them and holding their wings closed as they continue to walk about the

114   habitat; (3) males release females and rapidly move immediately in front of them at close

115   distance (<5 mm), where they present their colourful wings and faces; (4) either the sequence

116   returns to (2) with male re-straddling females, they mate, or (most often) they disperse. The

117   second stage—straddling—thus offers males the opportunity to assess the environment and their

118   orientation within it, while the third stage is when their decision to display at a given location

119   and orientation is realised and is therefore the focus of our observations as detailed below.

120   We observed courtships in a population of *L. cana* that inhabits the supralittoral zone of

121   Toowoon Bay, NSW, Australia (33.36 S, 151.50 E), in September and October of 2019. During

122   each courtship, we recorded the orientation of the male during the display phase (described

123   above; Fig. 1) of their ritualized dance, which we observed at a distance of 1-2 m. Courting pairs

124   were haphazardly selected during slow, repeated walks by an observer along a 255 m transect at

125   a distance of 5-10 m from the shoreline. Once a courtship naturally terminated with both parties

126   dispersing, we placed a straight marker at the males' final position in alignment with their medial

127   body axis, before recording the markers' orientation to the nearest one degree using a digital

128   compass, as well as the time. To initially validate the accuracy of this approach we tested it

129   against a video-based method in which male orientations were extracted from still-frames taken

130   from 25 video-recorded courtships (with a GoPro Hero 6 at 30fps) in which a compass was

131   visible in-frame. We found a strong correlation between orientations collected from video versus

132   direct observation (Pearson's r = 0.88), so we favoured the latter method for its convenience in

133   garnering a large sample size.

134   Once courtships were observed, we used the time and location data to calculate the solar

135   azimuth and elevation during every courtship via the package 'suncalc' (v. 0.5.0; Thieurmel and

136   Elmarhraoui 2019) for R (v. 3.6.0; R Core Team 2018). We then converted our circular measure

137   of male display orientations to a linear measure of the absolute deviation of each display from

138   the sun's azimuth. This gives a value between 0-180°, with 0° being a male displaying exactly

139   toward sun, and 180° directly away from it. We ignore the position of females since they remain

140   approximately opposite males at < 5 mm distance during displays (Fig 1).

141   To test the extent to which males can and do orient their displays we used the general

142   procedure above across three conditions, both observational and manipulative. In the two

143   observational conditions we recorded displays between the hours of 0730-1630 either on days of

144   full direct sunlight (n = 451 observations across six days), or heavy cloud with the sun

145   completely obscured (n = 227 across three days). For the manipulative assay we repeated the

146   procedure as for full sun conditions but obscured any direct sunlight using a static black plastic

147   sheet (Monarch pty. ltd) suspended on four aluminium poles ca. 10 m from the shoreline. This

148   cast a ca. 3 x 3 m shadow throughout a given day, and we recorded only courtships that began

149   and finished within this shaded area (n = 191 across three days). The broader environmental

150   conditions were similar across days within treatments (summarised in supplementary table S1)

151   and is partially accounted for in our statistical analyses (below).

152

Solar orientation and signal luminance

154   To model the effects of male orientation on the salience of their signals we first recorded

155   vector irradiances at the study site in 10º increments from 0º (directly toward the sun) to 180º

156   (directly away) at 0800, under representative conditions of full sunlight and heavy cloud. We

157   collected all spectra using an OceanInsight JAZ spectrophotometer with cosine-corrector and

158   oriented the 180º collector perpendicular to the ground (i.e. in the same plane as male faces and

159   wings during display). We then recorded the facial and whole-wing reflectance of 50 male *L.*

160   *cana* using the JAZ with its pulsed-xenon light source, at an integration time of 40 ms and a

161   boxcar width of 2. We used a bifurcated probe to both deliver and collect light, which we

162   oriented normal to the face and wing planes at a working distances of ca. 5 mm. These spectra

163   were lightly LOESS smoothed before being averaged to generate a representative male facial and

164   whole-wing reflectance spectrum (Fig. S1).

165   We then estimated how the luminance of male wings and faces varies as a function of

166   male orientation toward the sun. Here and throughout we focus on luminance alone given its

167   importance over chromaticity (hue and saturation) for mating (White et al. 2020). To do so we

168   calculated the integrated product of solar irradiance at each 10º increment from the solar

169   azimuth, male facial or wing reflectance, and the Rh1-6 'achromatic' receptor absorbance of

170   *Musca domestica* (as the nearest analogue to *Lispe*). We conducted all spectral processing and

171   visual modelling using lightr v1.1 (Gruson et al. 2019b) and pavo v2.4.0 (Maia et al. 2019) for R

172   v3.6.1 (R Core Team 2018).

173

174   **Statistical analyses**

175   To estimate whether male *Lispe cana* bias the orientation of their sexual displays toward

176   the sun we used a generalized linear mixed-effect model fit by restricted maximum-likelihood,

177   with Gaussian error and an identity link function. We specified male deviation from the solar

178   azimuth (0-180) as the response which we square-root transformed. We did so after our

179   inspection of errors from an untransformed model suggested slightly non-normal and

180   heteroscedastic residuals, which were improved to within acceptable margins (as visually

181   assessed) following transformation.

182   We specified the interaction between experimental condition (sun, cloud, and sun-

183   blocked) and solar elevation as a fixed effect, along with the main effects of each. If males do

184   actively orient their displays the result should be a negative effect of the full sunlight condition

185   on male display offset (i.e. a tendency toward smaller offsets from the solar azimuth in full sun),

186   when compared to the cloud and sun-blocked conditions. Our inclusion of solar elevation tests

187   for reduced display accuracy at higher solar elevations when the sun's azimuth is less readily

188   discerned. Such an effect would only manifest under conditions of full sunlight when any

189   display-orienting takes place, however, hence its inclusion via an interaction term. We specified

190   the Julian date on which each measurement was taken as a random effect to account for variation

191   associated with unmeasured within-day variables, such as broader climatic conditions.

192   To estimate the effects of male display orientation on signal luminance we first ran

193   generalised additive models (GAM) fit by restricted maximum-likelihood, with the offset from

194   solar azimuth (in 10° increments) as the lone predictor of signal luminance. The four resulting

195   models describe the possible variation in male facial and wing luminance as a function of their

196   sexual display orientation, during conditions of full sun and heavy cloud. We then used the

197   results of the full-sun GAM alone to predict the luminance of male signals at their actual

198   recorded orientations in both full-sun and heavy cloud conditions. We used only the full-sun

199   GAM after finding no relationship between signal luminance and orientation under heavy cloud

200   (Fig. 3d), and thus no possible benefits for signal salience to orienting toward the sun in such

201   conditions (see results). We then used Kruskal-Wallis rank sum tests, with eta^2 as an effect size,

202   to estimate the difference in achieved luminance between male displaying under full sun and

203   heavy cloud, with their luminance predicted from the full sun GAM. This, in effect, answers the

204   question of what males achieve by orienting their displays under ideal conditions.

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206   **Data availability**

207   All raw data and code are available via GitHub (https://github.com/EaSElab-18/ms_sunnyflies)

208   and will be persistently archived upon acceptance.

209

210   **Results**

211   We found clear differences in the orientation of male sexual displays across conditions

212   (Fig. 1; Fig. 2). A likelihood-ratio test on the overall model identified a significant effect of

213   experimental treatment alone (χ^2 = 86.86, df = 2, p <0.001), with no evidence for an effect of

214   solar elevation (χ^2 = 2.54, df = 1, p = 0.111) nor any interaction between treatment and solar

215   elevation (Fig. 3; χ^2 = 0.81, df = 2, p = 0.665). Individual estimates (Table 1) show this was

216   chiefly driven by a bias toward smaller angular offsets by displaying males under full-sun

217   conditions alone (est = -3.11 ± 1.136, df = 9, t = -2.74, p = 0.02). Male displays were oriented

218   toward the sun at a median offset of 44º ± 38 s.d. on days in which it was fully visible. But this

219   effect was absent in conditions of heavy cloud (87º ± 50 s.d.) and artificially obstructed sunlight

220   (96º ± 52 s.d.), which did not statistically differ from one another.

221   Our GAMs showed that the luminance of male wings ($F_{7.94}$ = 356, p < 0.001) and faces

222   ($F_{7.94}$ = 355.50 p < 0.001) follow a near-identical sigmoidal relationship with solar orientation

223   when illuminated in full sunlight (Fig. 4c). They are maximally luminant at 0º from the solar

224   azimuth, inflect at ca. 45º (95% CI = 37-53º faces, 43-47º wings), before reaching their minima

225   at ca. 80º. The luminance of wings, as compared to faces, varied across a slightly compressed

226   range owing to their reduced reflectance (supplementary Fig. S1), but was otherwise strongly

227   correlated with facial luminance. This effect was entirely absent in conditions of heavy cloud

228   (Fig. 4d), as we found no relationship between either of facial (F_1 = 0.190, p = 0.669) or wing (F_1

229   = 0.192, p = 0.667) luminance and solar orientation.

230   Our subsequent test of signal luminance during actual male displays suggest clear

231   benefits to active solar orientation in full sun. Both their faces (χ^2 = 86.97, df = 1, p < 0.01, η^2 =

232   0.127) and wings (χ^2 = 86.70, df = 1, p < 0.01, η^2 = 0.126) were subjectively brighter, with an

233   approximately four-fold increase as a result of their active display orienting. Given the absence

234   of a relationship between signal luminance and solar orientation under heavy cloud (as above),

235   any active orientation by males could yield no benefits to signal salience in such conditions.

236

Discussion

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238   The intensity and composition of sunlight shapes the salience of visual signals, and

239   selection should favour its flexible use. Here we tested this prediction in the cursorial fly *Lispe*

240   *cana* whose structurally coloured faces and wings are central to their ritualised courtship

241   displays. Our field-based observations show that males bias the orientation of their signals

242   toward the sun under clear skies, with individuals displaying at approximately 44º offset from

243   the solar azimuth on average. This degree of precision is maintained throughout the day

244   irrespective of solar elevation. Notably, however, the directional bias in displays broke down in

245   conditions of heavy cloud, and we were able to reconstruct this effect by experimentally

246   obstructing the sun under otherwise-ideal conditions. Our visual modelling of signal luminance

247   identified clear benefits to male display behaviour, with an approximately four-fold difference in

248   the fly-subjective luminance of male signals across the 180º range of possible orientations. These

249   combined results offer causal evidence that male flies actively orient their conspicuous displays

250   toward the sun, with tangible consequences for the salience of their structurally coloured signals.

251   Below we consider our findings in turn and discuss their relevance for communication efficacy

252   and signal evolution more broadly.

253   One immediate question is how male *L. cana* reliably orient their displays throughout the

254   entire day. The sun is the brightest spot in the sky so tracking its position directly is an obvious

255   solution, and this information can be supplemented through the use of indirect cues such as

256   intensity, chromaticity, and polarization gradients. On clear days, the intensity of sunlight

257   increases predictably toward the solar azimuth and atmospheric scattering means the sky is

258   relatively richer in long-wavelength light in the solar, as opposed to anti-solar, hemisphere (Fig.

259   3a; Coemans et al. 1994). The degree of polarisation is similarly graded and increases with the

260   angular distance from the sun (Coemans et al. 1994). The integrated use of such cues is well

261   described among insects, including flies (Philipsborn et al. 1990; Weir and Dickinson 2012),

262   albeit typically in the context of navigation. Monarch butterflies, for example, rely on direct and

263   indirect skylight cues to calibrate their time-compensated sun compass during annual migrations

264   (Heinze and Reppert 2011; Reppert et al. 2016), while desert ants integrate solar intensity,

265   chromaticity, and polarisation during navigation to and from the nest (Müller and Wehner 2007;

266   Lebhardt and Ronacher 2015).

267   Though our results cannot directly test whether male *L. cana* make use of all available

268   cues when orienting, the suppression of their orientation bias with the obstruction of direct

269   sunlight—both artificial and natural—suggests that they first and foremost rely on the sun's

270   immediate position. This follows from the fact that gradients in each of polarization, and (to a

271   lesser extent) luminance and chromaticity are present even when the sun is not directly visible,

272   and many flies are able to use this information to guide behaviour in other contexts (Philipsborn

273   et al. 1990; Weir and Dickinson 2012). However, while there is reason to expect that males

274   *should* be able to orient their displays in non-optimal conditions, our modelling suggests that

275   there is no benefit in doing so. Signal luminance bears no relationship to solar orientation under

276   heavy cloud (Fig. 3d), so males should instead prioritise more consequential effects such as the

277   selection of suitable display backgrounds (White et al. 2020). Whether they do so remains to be

278   tested.

279   The importance of accurate solar orientation during courtship is heightened by *L. cana*'s

280   use of structurally coloured ornaments. This is particularly true for wing interference patterns,

281   the colour and luminance of which is a product of thin-film interference from the layering of

282   chitinous wing membranes (Shevtsova et al. 2011). Since these colours are highly specular (i.e.

283   dominated by mirror-like reflection) in nature, the absence of a point-source illuminant such

284   as the sun can render the patterns indistinguishable (Shevtsova et al. 2011). Males that are less

285   able to optimise their orientation would therefore suffer penalty not only in the quality of their

286   wing colouration (e.g. via reduced intensity), but the 'category' too, as the patterns will be

287   entirely absent at oblique illumination angles.

288   Since males' wings are also semi-transparent, their optimal appearance is equally

289   dependent on the background against which they are presented. Dark backgrounds—such as

290   seaweed common to the foreshore habitats of *L. cana*—are fit for purpose, as they minimise

291   transmitted light which would overwhelm the weakly reflective interference patterns. Recent

292   work has documented just such an effect with males preferentially displaying against darker

293   visual backgrounds, and the magnitude of signal/background contrast predicting mating success

294   (White et al. 2020). Though we did not track mating success here a comparable effect on fitness

295   is plausible, given that imprecision in either background selection or orientation relative to the

296   sun will produce a similarly diminished signal (Fig. 4c). It remains to be seen whether and to

297   what extent the sun's position and visual backgrounds are weighed and integrated during

298   courtship, but the accumulating evidence paints a striking picture of behavioural flexibility in

299   service of communication efficacy.

300   The behaviours dedicated to the presentation of iridescent faces and wings imply an

301   important role for the latter in sexual communication, though their precise function is as-yet

302   unresolved. As structurally coloured ornaments the macro-scale appearance of faces and WIP's

303   is closely tied to the nanoscale organisation of underlying structures (Kinoshita 2008). If males

304   differentially vary in their ability to secure the conditions and/or material required to generate

305   such highly organised tissues, then the expression of facial and wing signals may be condition

306   dependent (Zahavi 1975; Keyser and Hill 1999; Shawkey et al. 2003).

307   In *Lispe cana* the male's UV-white are a product of incoherent scattering by modified

308   bristles (unpublished data, see Frantsevich and Gorb 2006 for details in a sister species), the

309   brightness of which will largely depend on the size and density of scatterers (Giraldo and

310   Stavenga 2007; White et al. 2012; Stuart-Fox et al. 2018). The appearance of their wing

311   interference patterns is instead a product of coherent scattering, as noted above, with colour

312   differences across the wing surface chiefly determined by variation in the thickness of the

313   cuticular thin-films (Shevtsova et al. 2011). Both are constructed and fixed during ontogeny

314   using the pool of resources gathered during the larval stage, and so their final appearance may

315   reflect individual variation in foraging ability and condition more generally (e.g. Kemp 2008;

316   Kemp and Rutowski 2007). Recent meta-analytic evidence supports the potential for condition-

317   dependent expression among structural colours in general (White 2020), and also suggests that

318   the greater organisation demanded by coherent, as opposed to incoherent, scatterers makes them

319   particularly suitable as condition-dependent ornaments. This argues for WIPs as more probable

320   vectors of information on mate quality in *L. cana* than faces, with the latter potentially serving as

321   signals of sex or species identity. Despite convincing evidence for sexual selection in WIP

322   evolution (Katayama et al. 2014; Hawkes et al. 2019), however, direct tests of their function as

323   signals remain outstanding.

324   In addition to iridescent ornaments as conduits of information, a non-exclusive possibility

325   is that male behaviour is itself informative of mate quality. Courtship displays are likely to be

326   energetically costly as the cycle of pursuing, straddling, and displaying with a given female is

327 often repeated several times before a clear outcome is achieved. Males clearly vary in their

328 ability achieve and sustain optimal orientations during courtship (Fig 2). If this variation is

329 dependent on male condition or 'quality' then their coloured ornaments may simply serve as

330 amplifiers of their behavioural performance. Displays against sub-optimal backgrounds or at

331 imprecise solar orientations would be readily apparent, particularly in the appearance of WIPs

332 (Shevtsova et al. 2011). Potential benefits to selective females are predictable since, as predators,

333 flight ability is central to prey capture in *L. cana* (Steidle et al. 1995; Pont 2019). This form of

334 condition-dependent variation in courtship effort, and corollary benefits to choosy viewers, is

335 well documented (Kotiaho 2000; Wagner and Hoback 1999; Jennions 1998). Similar effects are

336 known for variation in the precision of displays, such as in the quality of courts constructed by

337 bowerbirds (Endler et al. 2010; Kelley and Endler 2012), and the combination of limited-view

338 iridescence and precision displays in *L. cana* creates potential for a similar dynamic.

339 Our results extend a growing body of evidence which suggests extensive coevolution

340 between signals and display behaviours (Endler 1991; Endler and Thery 1996; Dakin and

341 Montgomerie 2009; Bortolotti et al. 2011; Sicsu et al. 2013; Klomp et al. 2017; White 2017;

342 Simpson and McGraw 2018). Notably, the strength of this link appears to vary with the extent of

343 fluidity in signalling environments and/or signals. That is, signals and environments which vary

344 dynamically across fine temporal or spatial scales are frequently coupled with flexible

345 behaviours to enhance the efficacy of information exchange. Iridescent signalling systems—such

346 as that examined here—fall at one extreme, with examples from insects (White et al. 2015), birds

347 (Endler and Thery 1996; Dakin and Montgomerie 2009; Simpson and McGraw 2018), and

348 guppies (Endler 1991) revealing considerable plasticity in display behaviour for optimising

349 signal delivery. Environments which vary unpredictably across fine spatial and temporal scales

350   appear to favour similar adaptive solutions. The foreshores of *L. cana* offer a case in point, since

351   a single wave can add or remove tracts of seaweed which the flies use for shelter and signalling,

352   and thus entirely restructure their immediate visual environment.

353   Despite these few well-defined examples, the extent to which we can we can predict any

354   one of behaviour, habitat structure, or signal design from knowledge of the others is a long-

355   standing question (Poulton 1890; Lythgoe 1988; Endler and Thery 1996). One key to resolving

356   this challenge is a deeper appreciation of the spatio-temporal complexity of visual

357   communication. Exciting advances continue to be made in defining and integrating the spectral

358   (Maia et al. 2019; van den Berg et al. 2019), spatial (Caves et al. 2018; Stoddard and Osorio

359   2019), and temporal (Gruson et al. 2019a) features of signal production and perception, and

360   systems such as *Lispe cana* offer a promising context for empirical progress.

361

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364

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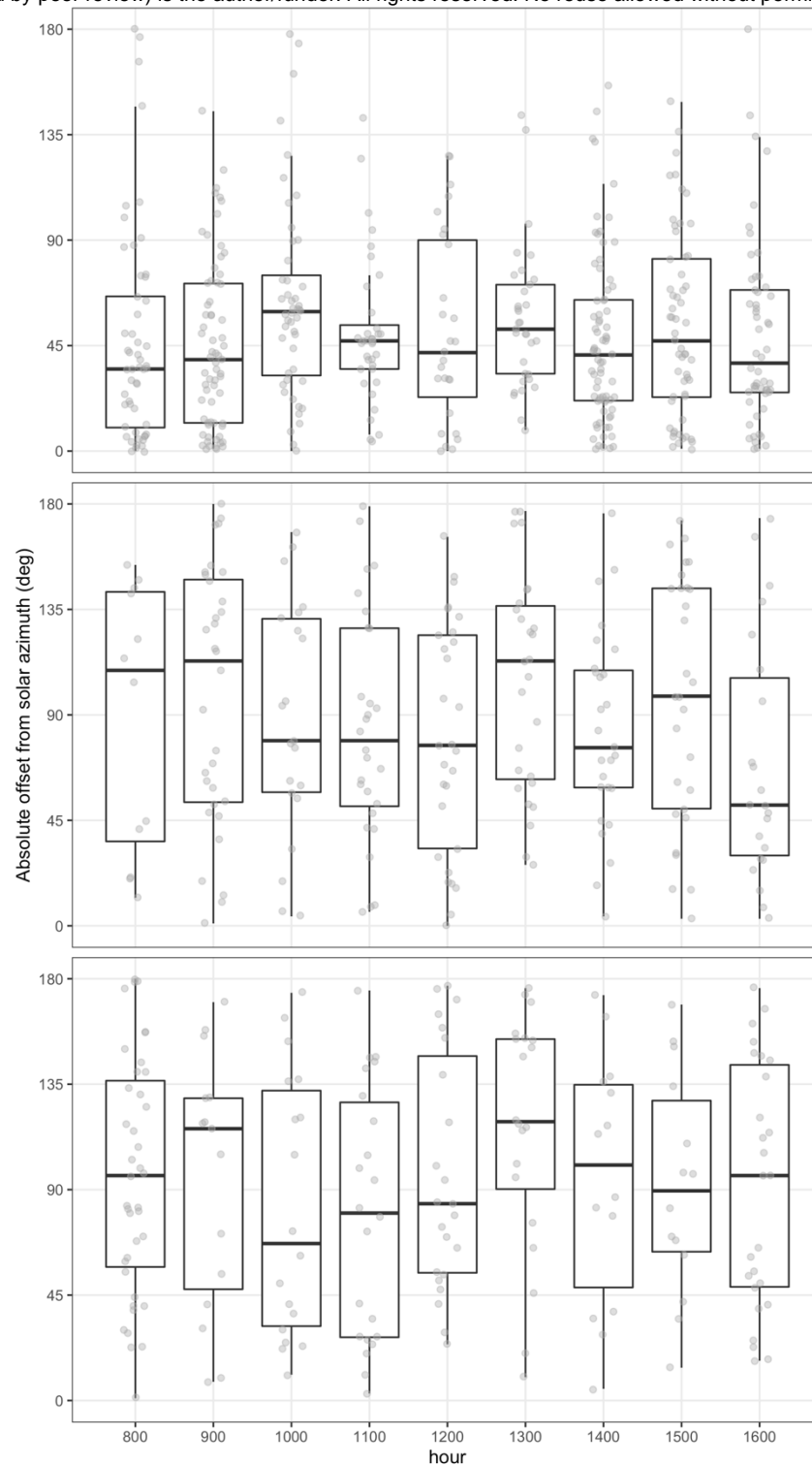
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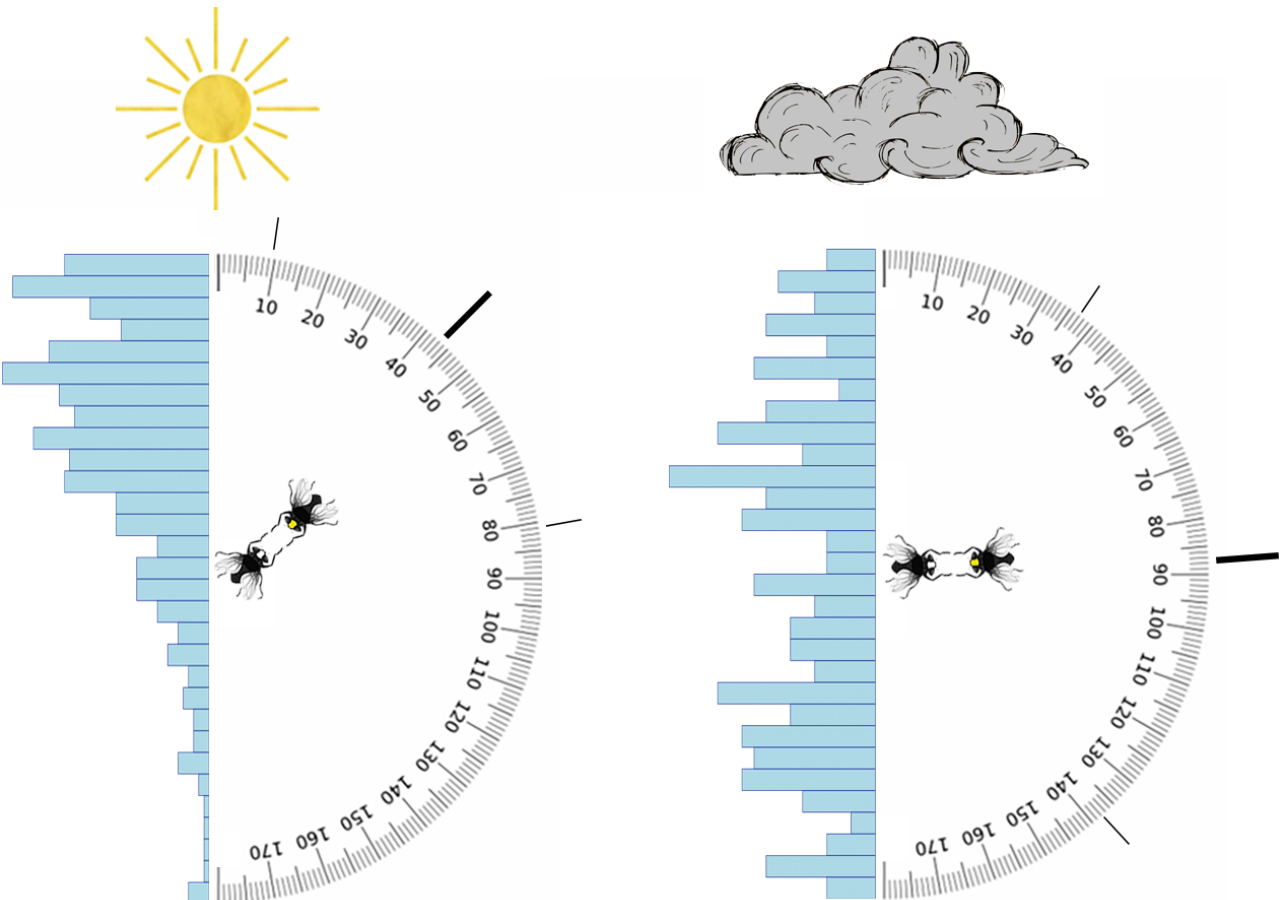
Figure 1: The orientations of *Lispe cana* during courtship displays under full sun (left) and heavy cloud (right). When displaying, male flies (white face) position themselves immediately in front of females (yellow face), and twist their wings forward in a seemingly ritualized 'dance'. Angles denote the offset of the male midline from the solar azimuth during courtship, with 0° representing a display directly toward the sun, and 180° directly away. Histograms show the distribution of male offsets from the sun under both conditions (n = 450 full sun, n = 227 heavy cloud), with the median ± standard deviation indicated by solid lines.

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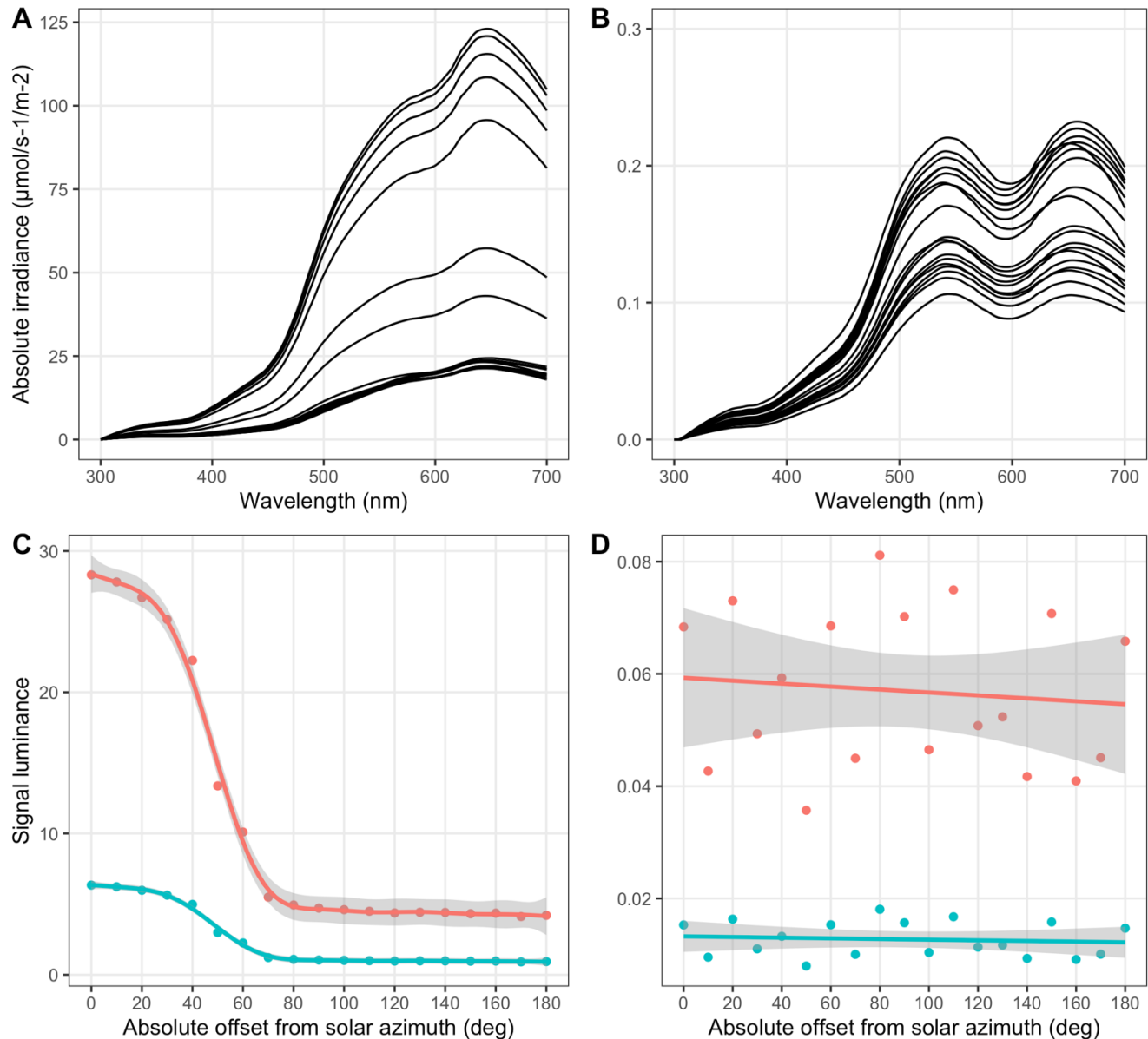546

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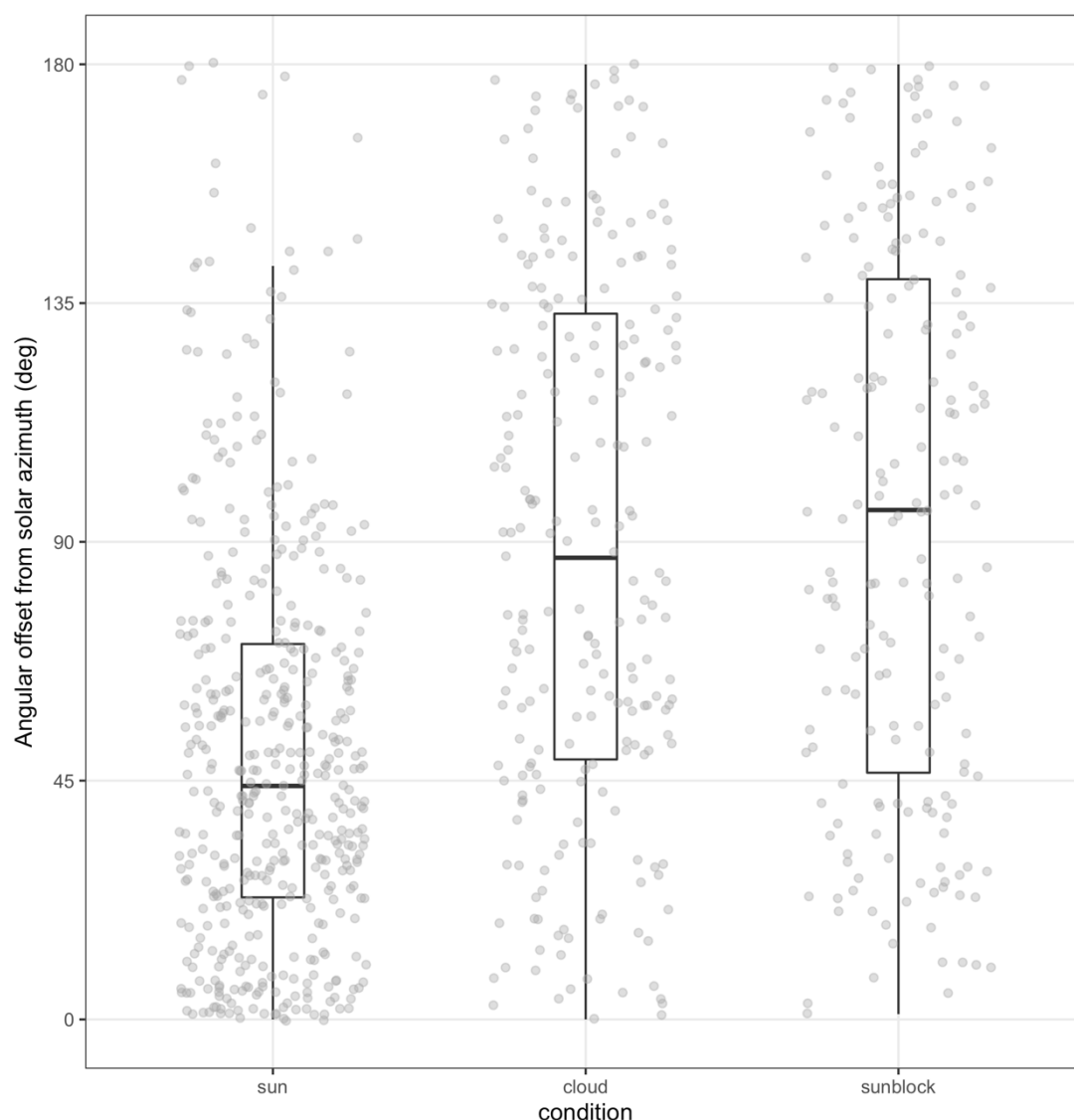
Figure 2: The orientation of displaying male *Lispe cana* with respect to the sun in conditions of full sun, heavy cloud, or experimentally obscured sunlight. Orientations are expressed as offsets from the solar azimuth, pooled across the 0730 - 1630 observation period, with 0° representing males presenting their iridescent signals directly toward the sun and 180^0 directly away.

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Figure 3: The orientation of displaying male *Lispe cana* in conditions of full sun (top), heavy cloud (middle), or experimentally obscured sunlight (bottom), pooled into hourly periods. Orientations are expressed as offsets from the solar azimuth, with 0° representing males presenting their iridescent signals directly toward the sun and 180^{0} directly away.

Figure 4: Solar irradiance and male signal luminance as a function of solar orientation. Solar irradiance in conditions of (a) full sun and (b) heavy cloud, recorded at 0º - 180º offset from the solar azimuth in 10º increments. Below is the luminance of male faces (red) and wings (green) across the same angular range, as modelled under full sun (c) or cloud (d). Lines denote generalised additive model fits ± standard errors. Not differing y axes across all panels.

589 **Table 1:** Parameter estimates and summary statistics from a generalised linear mixed
590 model examining the predictors of male display orientation in *Lispe cana.* Included are the
591 experimental condition (full sun, heavy cloud, and artificially obscured sunlight) and solar
592 elevation. Julian date was included as a random effect with a variance of 0.301. Full model
593 conditional R^2 = 0.169.

Fixed effects	Estimate	SE	df	*t*	*p*
intercept	8.389	0.771	853	10.88	< 0.001
condition (sun)	-3.115	1.336	9	-2.743	0.023
condition (sunblock)	0.425	1.014	9	0.419	0.685
solar elevation	0.011	0.016	853	0.712	0.476
condition (sun) x solar elevation	0.014	0.023	853	0.624	0.533
condition (sunblock) x solar elevation	-0.003	0.020	853	-0.191	0.849

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