Flies exploit predictable perspectives and backgrounds to enhance iridescent signal salience and mating success

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Abstract

Communication requires both the encoding of information and its effective transmission, but little is known about display traits that primarily serve to enhance efficacy. Here we examined the visual courtships of *Lispe cana*, a cursorial fly that lives and mates in heterogeneous foreshores, and tested the prediction that males should seek to enhance signal salience and consequent fitness through the flexible choice of display locations. We show that courting males access the field of view of females by straddling them and holding their wings closed, before moving ahead to present their structurally coloured faces in ritualised dances. Males preferentially present these UV-white signals against darker backgrounds, and the magnitude of contrast predicts female attention, which in turn predict mating success. Our results demonstrate a striking interplay between the physical and attentional manipulation of receivers and reveal novel routes to the enhancement of signal efficacy in noisy environments.

Introduction

Communication requires the effective transmission and reception of information in complex natural environments. Selection has favoured diverse solutions to this basic challenge, which are showcased among the visual ornaments and displays of animals (Dalrymple et al. 2018; Maia et al. 2013; Girard et al. 2015; White 2018). The functions of traits involved in sexual communication are twofold. Namely; to encode information relevant to mate choice and assessment (i.e. signal content) and ensure its effective transmission and reception (i.e. signal efficacy). Extensive work on content has shown how colour signals and (to a lesser extent) behaviours can encode information on benefits to potential mates, and are the targets of pre-copulatory choice (Brooks and Endler 2001; Kemp 2008a; Kemp 2008b; Barry et al. 2015). This is well illustrated in the literature on pigmentary colour expression and individual condition. The production of carotenoid-based signals, for example, can be physiologically tied to past or present body condition, reproductive and parental quality, and/or immune function, and so offer an honest guide to aspects of mate quality (Weaver et al. 2018). Less is known, however, about the features of displays that act primarily in the service of efficacy.

Most signalling traits are multifunctional (Candolin 2003; Bro-Jørgensen 2010). In addition to encoding information, colour patterns and displays may capture attention (Ord and Stamps 2008), amplify the conspicuousness of other traits (Smith et al. 2009), or modify the content of co-expressed signals (Endler et al. 2014). Traits that serve such purposes are not the target of choice but are nonetheless key determinants of attractiveness. This is particularly true in heterogeneous environments which will modify, and set limits on, the salience of signals, and the outcomes of selection for efficacy under such conditions are broadly predictable. In evolutionary terms, signal forms that best cut through noise to stimulate receivers will be favoured (Dusenbery

66 1992). Structural colours, which arise from the selective reflection of light by nano-scale
67 structures, offer one such solution since they are capable of generating uniquely broad, rich, and
68 dynamic colour palettes (Greenewalt et al. 1960; Vigneron and Simonis 2010; White et al. 2012;
69 Maia et al. 2013), and are evolutionarily labile (Maia et al. 2013; Wasik et al. 2014). Of particular
70 interest to this study is their potential for extreme chromaticity and brightness, which are valuable
71 for maximising basic features of efficacy such as signal conspicuousness (Schultz et al. 2008) and
72 detectability (Schultz and Fincke 2009) in the wild. In ecological terms, environmental complexity
73 can drive flexible behavioural solutions that improve the signal-to-noise ratio. These include the
74 precise behavioural delivery of signals (White et al. 2015; Simpson and McGraw 2018), varying
75 the timing and duration of displays (Poesel et al. 2006), and selecting optimal locations for
76 courtship (Endler and Thery 1996).

77 Flies possess a suite of colour-producing mechanisms and display behaviours and so offer
78 excellent, albeit underutilised, opportunities for exploring questions of signal evolution (Marshall
79 2012). The genus *Lispe* is a cursorial group of muscids that spend much of their life on or near the
80 ground in littoral habitats (Pont 2019). This includes courtship, during which males pursue and
81 physically straddle walking females before presenting their iridescent faces and wings in ritualised
82 'dances' (Frantsevich and Gorb 2006; Pont 2019). Though excellent work continues to document
83 the structure of these and related displays (Spofford and Kurczewski 1985; Frantsevich and Gorb
84 2006; Jones et al. 2017; Butterworth et al. 2019), it is not known whether or how such colours and
85 behaviours serve to effectively transmit information to mates. Given that the visual structure of
86 seaweed-dominated foreshores will vary over short temporal and spatial scales (e.g. with tides),
87 theory predicts functional links between signal structure and display behaviours to enhance signal
88 salience (Lythgoe 1979; Dusenbery 1992). Specifically, selection should favour male colour traits

89 that are reliably conspicuous to conspecifics in their surrounds, and/or which are delivered via
90 flexible behaviours for exploiting locally optimal conditions.

91 Here we examine the courtship displays of the fly *Lispe cana* with a view to testing how
92 signal structure and display behaviour mediate communication efficacy and mating success. *Lispe*
93 *cana* is a species endemic to Australia that inhabits supralittoral (foreshore) habitats spanning the
94 east coast. Males and females have striking structurally-coloured 'white' and 'yellow' faces (Fig.
95 1), respectively, that are weakly iridescent across lateral viewing angles and more strongly so in
96 the dorsevental plane (unpublished data). They are active predators of other ground-dwelling
97 invertebrates and they live, hunt, and mate on shorelines (ca. 0-5 m from the waterline) which are
98 often populated by patchy distributions of seaweed and detritus (Fig. 1). The casual observation of
99 courtship in this species shows that smaller (5.5 - 7 mm body length) males approach and straddle
100 the larger (6.5 - 8 mm) females from behind, and hold the female's wings closed using their forelegs
101 (Fig. 2 a-b; supplementary video S1). Males maintain this position as females continue to move
102 about the environment. After a time, males rapidly move in front of females and present their
103 iridescent faces and wings in ritualised displays that consist of erratic movements around the
104 female's head at very close distance (Fig. 2c). These displays then typically terminate when
105 females lose interest and disperse, or when males re-mount and mate with receptive females (Fig.
106 2d). This presents ecologically tractable opportunities to examine the predicted links between
107 signal structure and signalling behavior in the service of efficacy, since the initial straddling of
108 mates implies the potential for males to optimise the timing and location of displays given their
109 largely shared field of view. In a field-based assay, we thus quantified the visual structure of signals
110 and signalling environments and tested the prediction that males should seek to maximise the

111 conspicuousness of their facial signals within their dynamic visual habitats to enhance mating
112 success.

113

114 Methods

115 *Sampling courtships, flies, and visual backgrounds*

116 We recorded 42 independent courtships of *L. cana* using a GoPro Hero 6 at either 30 or 60
117 fps in the field. From these we extracted the duration of the straddling and display phase of each
118 courtship, which are readily identified by eye (Fig. 2b-c). We also estimated the male-female
119 alignment and elevation of straddling males in three haphazardly selected frames from each
120 courtship sequence, which we averaged. Alignment was taken as the angle between male and
121 female midlines (e.g. with 0 indicating complete alignment) as measured from points on the centre
122 of their heads and abdomens from top-down video. Similarly, male elevation was taken as the
123 angle between male and female midlines from a lateral view. We were unable to extract complete
124 data for nine courtship sequences due to a lack of suitable viewing geometries.

125 All courtships were recorded within a 6 m^2 region of the supralittoral zone of Toowoon
126 Bay, NSW, Australia, on clear days between 1100 and 1300. We used a fixed region for our
127 observations so that we could subsequently sample the entirety of the visual environment for
128 analysis (detailed below), and restricted the observation period to hold the sun's azimuth
129 approximately constant, and so minimise any effects of light-source directionality on variation in
130 signal appearance and display behaviour. Flies typically dispersed outside the observation area at
131 the conclusion of a display, minimising the risk of repeated recordings, and the few that did remain

were not intentionally observed again. Following each display, we noted whether the interaction resulted in copulation, and collected a sample of the nearest piece of background material within 150 mm directly behind the courting male. If no such material was present, we took sand to be the relevant visual background. At the conclusion of the experiment we also gathered all material within the 6 m^2 observation area as a representative sample of the all possible visual backgrounds available to males. From these we collected reflectance measurements at three evenly spaced points along the length of each piece of material using the general method described below and averaged them. We also photographed the focal area at the conclusion of the experiment and estimated the proportional area of open sand using Adobe Photoshop CC (v20.0.6), before collecting haphazardly-selected samples for spectral measurement. By systematically collecting and measuring all material within the area of observation, and including spectral samples of sand proportional to its availability, we also approximately accounted for the relative abundance of potential viewing backgrounds in our analyses of background selection and bias (detailed below).

We also separately collected 17 male and 20 female flies and recorded the reflectance of their facial colouration to calculate a population-average estimate of facial colouration for use in our analyses of signal/background contrast. This was necessary because the rapid dispersal of flies at the conclusion of courtship meant we were unable to sample the observed courting pairs described above. We used an OceanOptics Jaz UV-VIS spectrometer with a pulsed xenon light source, set to an integration time of 50 ms with a boxcar width of five. We used a 400 um bifurcated probe oriented normal to the plane of each fly's face to capture the entirety of its ca. 5 mm^2 area, and recorded and averaged two measurements per individual. When measuring background material, we instead used a measurement geometry of 0° illumination and 45° collection to minimise specular reflections from damp surfaces. A spectralon 99% diffuse reflector (Labsphere,

155 New Hampshire) and black velvet served as our light and dark standards, respectively, and we
156 recalibrated between each measurement. Finally, we binned the resulting spectra at 1 nm intervals
157 and applied some minor locally weighted scatterplot (LOESS) smoothing (α = 0.15) prior to
158 analysis.

159

160 ***Visual modelling***

161 We used an early-stage (i.e. retinal-level) model of muscid colour vision to estimate the
162 subjective colour and luminance contrasts of male *Lispe* faces against presentation backgrounds.
163 We drew on the receptor sensitivities of *Musca domestica* as the closest available relative of *Lispe*,
164 and assumed the involvement of R7p, R8p, R7y, and R8y photoreceptors in chromatic processing,
165 and R1-6 receptors in achromatic processing (Hardie 1986; Troje 1993). For chromatic contrasts,
166 we drew on the model of Troje (Troje 1993) and estimated receptor quantum catches as the
167 integrated product of receptor sensitivity, stimulus reflectance, and a standard-daylight illuminant.
168 We then calculated the difference in relative stimulation between R7y-R8y and R7p-R8p receptors
169 as putative opponent channels that define the location of a given stimulus in dipteran colourspace
170 (Fig. 1, right side), and chromatic contrasts were taken as the Euclidean distance between stimuli
171 in this space. We estimated luminance contrast as the Weber contrast of fly faces against their
172 backgrounds, with quantum catches calculated as above albeit using the R1-6 receptor absorbance.
173 All spectral processing, analysis, and visual modelling was carried out using the package package
174 'pavo' v2.2 in R v3.5.2 (Maia and White 2018; R Core Team 2018; Maia et al. 2019).

175

176 ***Statistical analyses***

We first tested whether male flies display against visual backgrounds non-randomly with respect to their signal contrast. We used a bootstrap test which, for a given run, entailed drawing 42 backgrounds with replacement from the total pool of background material collected from the observation area, before calculating the mean of the chromatic and achromatic contrasts of the average male face against each item. We repeated these 5000 times, thereby generating a null distribution of contrasts that represent the probability of observing a given mean chromatic or achromatic contrast value under the assumption that males display against backgrounds at random. We then calculated the probability of attaining our observed chromatic and achromatic contrast values given this null expectation and used Cohen's d (the difference between sample and null means, divided by the pooled standard deviation) as an estimate of the magnitude of any difference between observed and null-distributed contrast values.

We then examined the effects of signal contrast and two proxy measures of female attention on mating success using generalised linear models in a restricted maximum likelihood information-theoretic framework (Anderson and Burnham 2004). We took the duration of male displays as a between-courtship measure of attention, because when males release females and move to present their facial signals (Fig. 2b-c) the duration of the subsequent display is largely under female control. Females are free to disperse at any point during the male display and so terminate it, which is indeed the most common outcome of a courtship interaction (Fig. 2d). Our second, within-courtship, measure of female attention drew on the fact that females repeatedly re-orient themselves in brief, saccadic movements during male displays (supplementary video). We therefore calculated the proportion of these reorientations that were directed toward displaying males, as defined by a reduction in the angle between the female midline and male head. A value of one indicates that all female movements were toward males during their displays, while a value

of zero means that females consistently oriented away from displaying males. Of course, these are only approximate measures, but the above rationale, and the correlation of both measures (Pearson's $r = 0.33$, $t_{40} = 2.22$, $p = 0.03$), suggest that they collectively capture relevant aspects of female attention.

We specified a global model with mating success as a binomial response (with logit link function), and included male display duration, the proportion of female reorientations toward displaying males, and chromatic and achromatic signal contrast as main effects. We examined all models containing linear combinations of these predictors along with an intercept-only null model and ranked them according to Akaike's Information Criterion (AICc, adjusted for small sample sizes). We calculated the R^2 for the most parsimonious model(s), as approximated by a ΔAICc of < 2 (Anderson and Burnham 2004).

We also examined the effect of signal contrasts and straddling duration on both the duration of male displays, and the proportion of female orientations toward displaying males (i.e. female attention). We modelled display duration as a Gaussian response (with identity link function) and female orientations as a binomial response (with logit link) and included chromatic and achromatic signal contrasts and the duration of the straddling phase as main effects in both models. We visually confirmed the assumptions of normality among residuals and homogeneous variance structures for all models and used the package 'MuMIn' v1.43.6 (Bartoń 2013) for all model selection in R (R Core Team 2018).

Results

During courtship male *L. cana* pursue lone females before straddling them and holding their wings closed with their forelegs (Fig. 2). While in this position, males are slightly elevated (29.4 ± 7.5^{o}) and closely aligned with the body axis of females (2.1 ± 1.4^{o}), and are afforded direct access to the female's field of view (Fig. 2b). This straddling phase lasted 1.58 - 16.53 seconds, after which females were released by males who then repeatedly ran in close semi-circles in front of females as part of a ritualised display (supplementary video; also see Frantsevich and Gorb 2006; Butterworth et al. 2019 for comparable examples). During these display phases which lasted 0.76 - 11.60 seconds, male *L. cana* preferentially presented themselves against backgrounds that generated strong achromatic ($p < 0.001$, $d = 3.363$) and chromatic (bootstrap $p = 0.047$, $d = 1.744$) contrast with their facial colouration (Fig. S1). That is, their faces appear much brighter and slightly more colourful to conspecifics than would be expected if they were displaying at random within their visual environments.

The most parsimonious model of mating success (12/42 courtships) indicated a strong positive contribution of both of our included measures of female attention; the total duration of male displays, and the proportion of female orientations toward displaying males (Table 1; Table 2). It clearly outperformed the null ($(w_1 + w_2)/w_{null} > 700$), and was approximately three times as informative as the second and third best models that included the additional effects of chromatic contrast (ΔAICc = 2.15, $w_1/w_2 = 2.93$) and achromatic contrast (ΔAICc = 2.44, $w_1/w_3 = 3.38$), respectively. This suggests that female attention (as measured via male display duration and female orientations) directly mediates mating success, which is further supported by the predictive relationship between achromatic, but not chromatic, signal contrast and both display duration and female orientations (Table 3; Fig. 4). The effect of signal/background luminance contrast on

243 mating success is thus almost entirely driven by its influence on female attention. That is, males
244 which presented more contrasting signals through the selective use of backgrounds were able to
245 display longer and better held females' focus, which improved mating success. Finally, we found
246 no effect of straddle duration on display duration or female orientations (Table 4), indicating that
247 the duration of the two courtship phases is unrelated and, more broadly, that female receptivity
248 during straddling and display phases is unrelated.

249

250 **Discussion**

251 Selection has generated myriad solutions to the challenge of communicating amidst noise,
252 with animals varying the location (Endler and Thery 1996), timing (Poesel et al. 2006), and
253 behavioural delivery (White 2017; Simpson and McGraw 2018) of signals to ensure their effective
254 reception. Here we reveal novel links between a structural colour signal and its behavioural
255 presentation, which in part relies on the exploitation of the receiver's predictable field of view.
256 Male *Lispe cana* straddle and align themselves with females during courtship, before releasing and
257 displaying their conspicuously coloured faces in a ritualised dance (Fig. 2). Males preferentially
258 display against darker backgrounds which enhances visual contrast (Fig. S1), leading to longer
259 display times overall and increased female attention toward male signals (Fig. 4) and, in turn,
260 enhanced mating success (Fig. 3). Our results suggest that males are flexibly exploiting females'
261 perspectives and visual environments to enhance the attractiveness of their complex displays and,
262 hence, mating success.

263 The courtships of *L. cana* reveal a striking interplay between the physical and attentional
264 manipulation of receivers. When straddling, males physically impede females from flying, and the

265 independence of straddling and display durations suggests that it proceeds until either (the
266 consistently larger) females forcefully disengage males, or males release to display (Table 1).
267 Whether males have any control over the mobility of walking females, or present an encumbrance
268 at all, is unclear, though the near-constant movement of females (pers. observation) means that
269 diverse display locations may be passively sampled within a short time. Once males do release
270 then females are physically free to leave, which necessitates the capturing of female attention
271 during signalling to ensure further receptivity and mating. The predictive relationships between
272 facial contrast and female attention (Fig. 3), and female attention and mating success (Fig. 4),
273 suggest a central role for male signals and presentation behaviours in maintaining the focus and
274 receptivity of females amidst cluttered visual environments. The structurally generated UV-white
275 colour of male faces will, by definition, maximise luminance contrast among the desaturated hues
276 of surrounding seaweed (Fig. 1; though less so among sand), and their flexible display behaviours,
277 combined with predictable knowledge of viewer perspectives, allow for the exploitation of locally
278 optimal conditions. Thus, males presenting greater luminance contrast are afforded longer displays
279 by viewing females as well as greater female attention during their displays, with tangible benefits
280 for mating success.

281 Several aspects of male displays are likely to further improve salience. For one, the rapid
282 movement of males from outside the female field of view to within it between straddling and
283 display phases (Fig. 2b-c) will generate strong temporal contrast. This may be amplified by the
284 adaptation of female receptors to visual backgrounds immediately prior to seeing the male display,
285 since the fastest component of receptor adaptation takes less than a second (Smirnakis et al. 1997;
286 Shevell 2001; Baccus and Meister 2002). The continual, erratic movement of males during
287 displays will also sweep out a larger area of the female's retina (supplementary video; unpublished

288 data), further enhancing its salience. Analogous display features are described in male great
289 bowerbirds *Ptilonorhynchus nuchalis*, which offer an illustrative comparison. Males construct
290 bowers and exploit the fixed perspective of females to induce a visual illusion, the quality of which
291 is predictive of male mating success (Kelley and Endler 2012). In addition to this focal display
292 males use foraged materials to colour the walls of their avenues and also actively flash coloured
293 objects across the female's field of view. Though not associated with mating success directly, these
294 latter features serve to increase communication efficacy through the capturing of receiver attention
295 and enhancement of other signals (Kelley and Endler 2012; Endler et al. 2014).

296 The strong effects of display duration and female orientations on mating success suggests
297 that females may be assessing content-rich features of the male display, since the informational
298 load of a task increases decision times (Chernev et al. 2015; Hemingway et al. 2019). Though not
299 directly explored here, the structurally coloured faces of male *L. cana* are theoretically well-suited
300 conduits of information on mate quality. This colouration is primarily a consequence of light
301 scattering by flattened bristles (Frantsevich and Gorb 2006), which demand close developmental
302 control during metamorphosis for optimal expression (Ghiradella and Butler 2009). Variation in
303 the resulting signal may thus inform potential mates about foraging ability, developmental
304 stability, and/or aspects of genetic 'quality' (Kemp 2008b; Barry et al. 2015). The primacy of
305 luminance over chromatic contrast in our tests (Table 1; Table 2) suggests a role for signal
306 brightness and variation therein as the more salient channel. It is also consistent with the relatively
307 under-developed colour sense of flies, which instead tend to draw on luminance to guide the
308 identification and categorisation of stimuli (Troje 1993; Lunau 2014). Though luminance is a less
309 reliable cue than hue in natural environments, it is a known channel of sexual communication in
310 several insect species (Kemp 2008a; Kemp 2008b; Barry et al. 2015). Well-described examples

311 include the mantid *Pseudomantis albofimbriata* in which the brightness of females abdomens is
312 tied to their current condition and is the focus of male choice (Barry et al. 2015), and the butterfly
313 *Eurema hecabe*, wherein the intensity of male UV wing colouration encodes information on larval
314 resource acquisition (Kemp 2008b; Kemp 2008a).

315 Despite the plausibility of *L. cana*'s faces as informative signals, we found no direct
316 relationship between visual contrast and mating success as might be predicted for traits under
317 selection for such a purpose. There are several reasons for this. For one, the role of any given trait
318 may be to hold attention, as our results show is at least partly the case (Fig. 4), with others acting
319 as more direct indicators of mate quality. The iridescent wing interference patterns of male *L. cana*
320 that are actively presented during displays offer one such candidate trait, and emerging evidence
321 suggests these patterns are both widespread among flies and may be subject to sexual selection
322 (Katayama et al. 2014; Hawkes et al. 2019). A closely related possibility is that male facial
323 colouration is an amplifier (Hasson 1991; Byers et al. 2010), which serves to make the direct
324 targets of choice easier to discern or assess. Alternately, if male facial colouration is instead a
325 signal of species or sex recognition, as suggested by the striking sexual dimorphism (Fig. 1) and
326 variation in facial colouration among sympatric species (Pont 2019), then female preferences may
327 be expressed as a simple threshold function. That is, the trait may have to be above a certain value
328 to be effective, but variation beyond that will be irrelevant. Finally, and more specific to this study,
329 is the fact that we averaged facial reflectance across a sample of flies that were not observed in the
330 focal courtships themselves, which prevents us from assessing the direct contribution of
331 individual-level signal variation (in addition to behavioural variation) to mating success.

332 Environments frequently modify, and set limits on, the salience of sexual displays. Here
333 we describe an innovative solution to this problem that relies on the physical and attentional

manipulation of viewers. By adopting the perspective of receivers during courtship, male flies are able to select locally optimal display locations to enhance the salience of their sexual signals and consequent mating success. More broadly, our results suggest that conspicuous signals and flexible display behaviours can arise in response to environmental heterogeneity. Display site properties will vary between habitats, however, which may mediate local adaptation and sexual isolation. This will be most pronounced between habitats that vary acutely in relevant aspects of structural complexity, such as the reliably seaweed-laden foreshore of our focal population, and the entirely barren beaches of nearby populations. This presents intriguing opportunities for illuminating the role of sexual communication in diversification, for which tractable groups such as *Lispe* hold excellent promise.

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Data availability

All data and code will be made persistently available upon acceptance.

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Figures and Tables

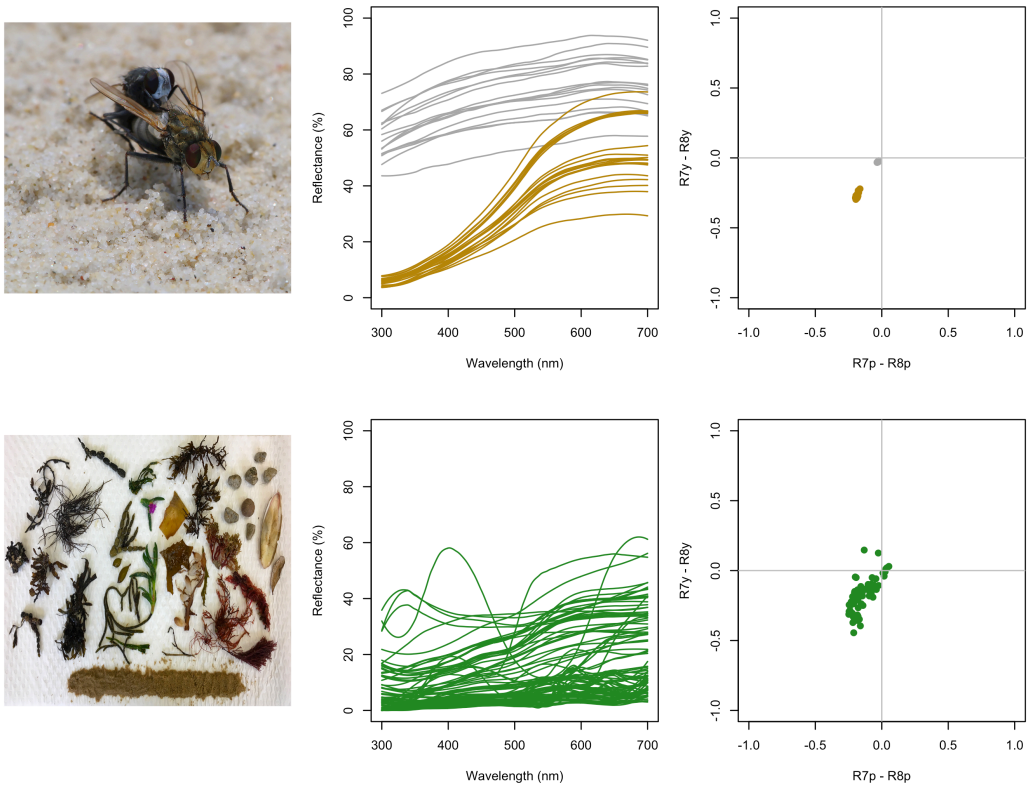

Figure 1: Male and female *Lispe cana* and material sampled from their foreshore habitats (left; photo credits NB & TEW), the reflectance spectra of male (grey) and female (yellow) faces and background material (centre), and the spectra as represented in a muscid colourspace (right).

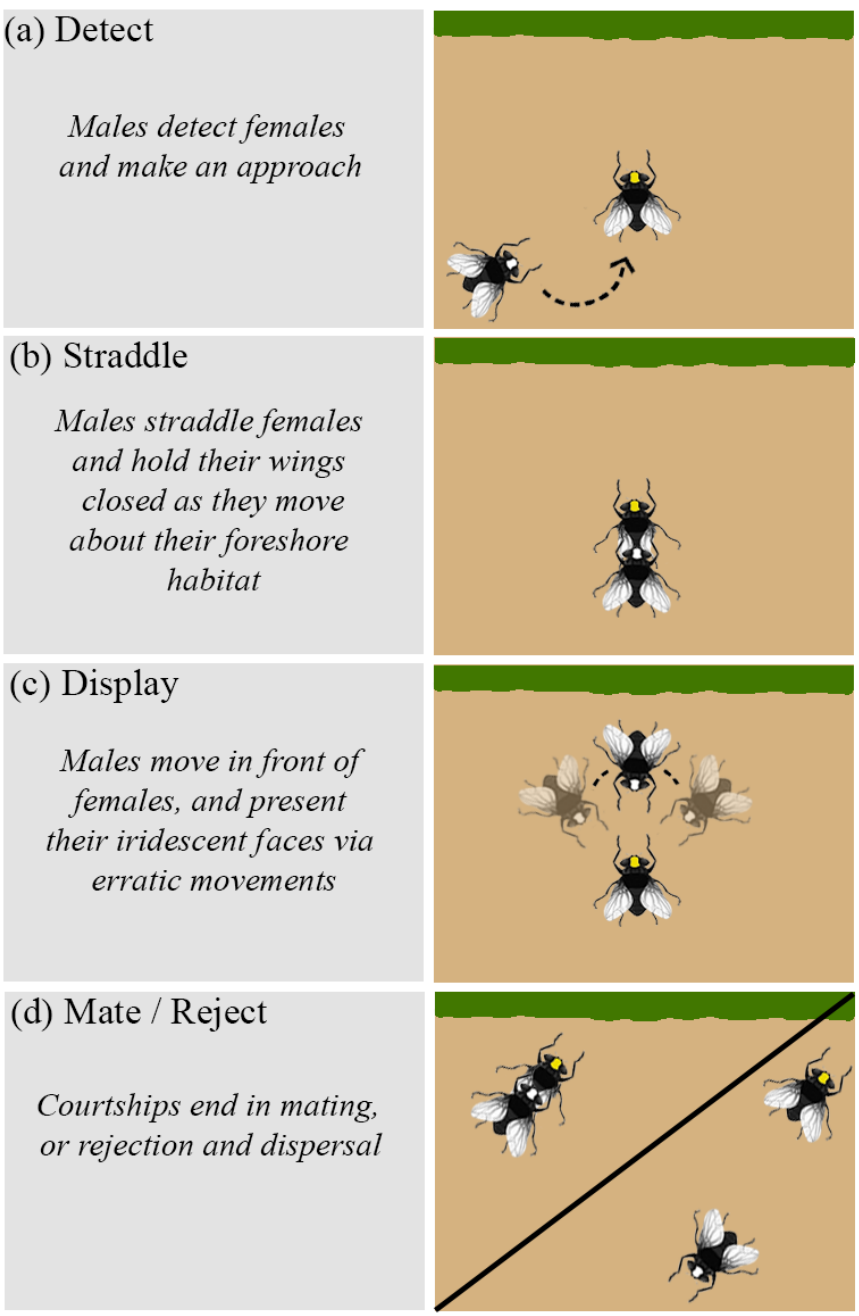

Figure 2: Courtship in the cursorial, shore-dwelling muscid fly *Lispe cana.* Male *L. cana* detect females within their seaweed-dominated habitats and rapidly approach (a), before 'straddling' females from behind and holding their wings closed (b). During this time males are aligned with females (2.1 ± 1.4° offset, 29.4 ± 7.5° elevation), and are thus sharing a field of view. Males then preferentially display against backgrounds that enhance the luminance contrast of their UV-white faces, which leads to improved salience, female attention and subsequent mating success.

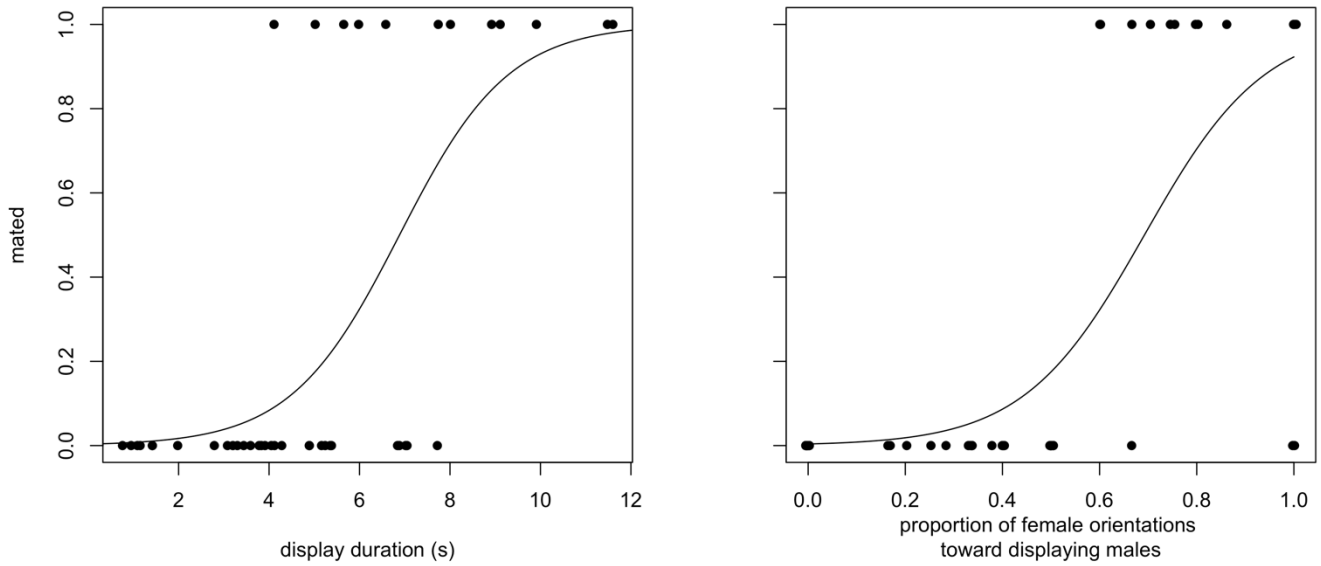

Figure 3: The relationship between two measures of female attention — display duration and female orientations toward male displays — and mating success in *Lispe cana*. Circles represent the presence or absence of mounting following courtship, with the line indicating model fit as estimated by a binomial GLM (Table 2).

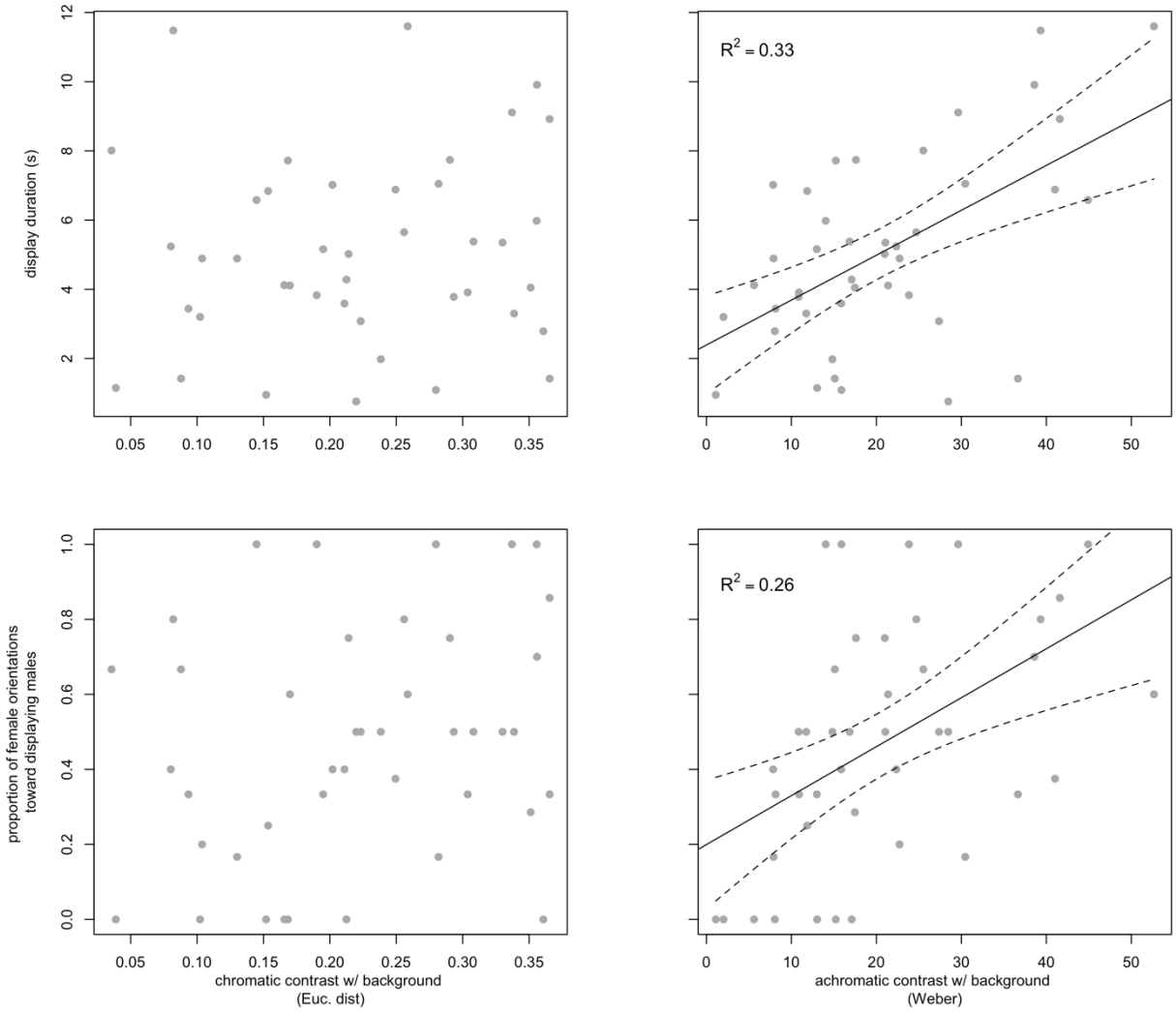

Figure 4: The relationship between the chromatic and achromatic facial/background contrast of male *Lispe cana*, male display duration, and female orientations toward displaying males. Solid and dashed lines indicate the best fit ± 95% CI as estimated by a GLM (table 3).

Table 1: Full model selection table, detailing the relative strength of candidate binomial GLM's for the relationship between mating success and one or more linear combinations of courtship display duration (dur), the proportion of female orientations toward males during displays (orient), and the chromatic (ΔS) and achromatic (ΔL) contrast of male facial colouration against their visual backgrounds.

model	d.f	LL	AICc	$\Delta AICc$	w
duration + orient	3	-6.16	19.00	0.00	0.57
duration + orient + ΔS	4	-6.02	21.10	2.15	0.20
duration + orient + ΔL	4	-6.16	21.40	2.44	0.17
duration + orient + ΔS + ΔL	5	-6.00	23.70	4.72	0.05
orient + ΔL	3	-10.85	28.30	9.37	0.01
orient + ΔS + ΔL	4	-10.74	30.60	11.60	0.00
orient	2	-13.65	31.60	12.64	0.00
duration	2	-14.76	33.80	14.86	0.00
orient + ΔS	3	-13.63	33.90	14.93	0.00
duration + ΔL	3	-13.84	34.30	15.34	0.00
duration + ΔS	3	-14.67	36.00	17.00	0.00
duration + ΔS + ΔL	4	-13.77	36.60	17.67	0.00
ΔL	2	-18.64	41.60	22.63	0.00
ΔS + ΔL	3	-18.63	43.90	24.94	0.00
null (intercept only)	1	-25.13	52.40	33.39	0.00
ΔS	2	-24.85	54.40	35.05	0.00

Table 2: Full results of the leading model of mating success that includes the effects of male display duration and the proportion of female orientations toward males during their displays, drawn from a global binomial GLM that included display duration, female orientations, chromatic contrast, and achromatic contrast as predictors (Table 1).

parameter	**estimate**	**std. err.**	**z**	**p**	**R^2**
intercept	-12.93	4.72	-2.74	< 0.001	0.68
display duration	1.14	0.54	2.10	0.035	
orientations	9.61	3.67	2.62	< 0.001	

Table 3: Results of separate GLM's estimating the effect of chromatic (dS) and achromatic (dL) face/background contrasts, and the duration of the 'straddling' courtship phase on two proxy measures of female attention: the duration of male *L. cana*'s courtship displays, and the proportion of female orientations toward males during their display.

model	parameter	est.	std. err.	t	p	R^2
display duration ~ $\Delta S + \Delta L$ + straddle duration	intercept	3.00	1.30	2.31	0.03	0.33
	ΔS	-0.66	3.81	-0.17	0.86	
	ΔL	0.13	0.03	4.20	< 0.001	
	straddle dur.	-0.06	0.09	-0.64	0.52	
female orientations ~ $\Delta S + \Delta L$ + straddle duration	intercept	-0.81	0.56	-1.44	0.15	0.26
	ΔS	1.25	1.59	0.79	0.43	
	ΔL	0.05	0.01	3.25	0.001	
	straddle dur.	-0.06	0.04	-1.44	0.15	