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Heightened condition dependent expression of structural coloration in the faces, but not wings, of male and female flies

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Abstract

Structurally colored sexual signals are a conspicuous and widespread class of ornament used in mate choice, though the extent to which they encode information on the quality of their bearers is not fully resolved. Theory predicts that signaling traits under strong sexual selection as honest indicators should evolve to be more developmentally integrated and exaggerated than nonsexual traits, thereby leading to heightened condition dependence. Here, we test this prediction through examination of the sexually dimorphic faces and wings of the cursorial fly *Lispe cana*. Males and females possess structural UV-white and golden faces, respectively, and males present their faces and wings to females during close-range, ground-based courtship displays, thereby creating the opportunity for mutual inspection. Across a field-collected sample of individuals, we found that the appearance of the faces of both sexes scaled positively with individual condition, though along separate axes. Males in better condition expressed brighter faces as modeled according to conspecific flies, whereas condition scaled with facial saturation in females. We found no such relationships for their wing interference pattern nor abdomens, with the latter included as a nonsexual control. Our results suggest that the structurally colored faces, but not the iridescent wings, of male and female *L. cana* are reliable guides to individual quality and support the broader potential for structural colors as honest signals. They also highlight the potential for mutual mate choice in this system, while arguing for 1 of several alternate signaling roles for wing interferences patterns among the myriad taxa which bear them.

Keywords: honest signal, iridescent, mate choice, sexual selection, wing interference pattern

Color patterns present a striking dimension of phenotypic variation, and nowhere is this better showcased than in the context of sexual communication. The variable ornaments of male guppies (Houde 1987; Endler 1991), iridescent signals of butterflies (Kemp 2008a; White et al. 2015), and exaggerated badges of hummingbirds (Greenwalt et al. 1960) are exemplars and have each served as models for examining the role of sexual selection in driving the evolution of conspicuous visual signals. A central hypothesis is that such signals are selectively favored as honest guides to the genetic and/or phenotypic quality of potential mates, with empirical tests primarily guided by costly signaling and index models (reviewed in Weaver et al. 2017). Costly signaling models such as the Zahavian handicap predict costs to signal production or maintenance, which are differentially borne among signalers (Zahavi 1975; Grafen 1990). Among-individual differences in the ability to acquire resources underlie differences in their ultimate allocation, with only the "best" individuals able to produce and bear the most brilliant signals. Indices, by contrast, describe how signal production is unfakably tied to the function of internal processes (Maynard-Smith 2003). The energy, resources, and/or time required for signal production are not costly unto themselves under such an explanation,

and honesty is instead maintained by direct links to core physiological processes. The expected outcome of both processes, which stands as the key test of theory, is that signals should exhibit heightened-condition dependent expression when compared with traits under weaker sexual selection (Cotton et al. 2004a).

Almost all color signals in nature are the product of absorption by pigments or scattering by nanostructures (Johnsen 2012). Empirical tests of honesty-based models have chiefly focused on the former, with carotenoid-based ornaments receiving particular attention (reviewed in Blount and McGraw 2008; Svensson and Wong 2011). As pigments that cannot be synthesized *de novo* carotenoids must be acquired through diet (Blount and McGraw 2008). This environmental dependence creates opportunity for selection to favor links between resource acquisition and allocation and, ultimately, signal expression. The red plumage of the house finch *Haemorhous mexicanus* offers a well-characterized example, with recent work revealing how the yellow-to-red bioconversion of dietary carotenoids prior to deposition links individual condition (via mitochondrial efficiency) to the quality of visual displays (Hill et al. 2019), which are used to inform mate choice (Hill 1994).

Structural colors, by contrast, arise from by an interaction between light and nanostructures that vary in refractive index, and are capable of degrees of brilliance and spectral richness otherwise unattainable through pigments alone (Vukusic and Sambles 2003). Despite their widespread use as conspicuous sexual ornaments, the case for honesty in structurally color signals is less well developed. There are 3 broad arguments regarding such potential. For one, if the construction and/or maintenance of nanostructures are materially demanding, then this may create a trade-off against other core needs (Zahavi 1975; Keyser and Hill 1999). Such demands will then be differentially met among individuals of varying quality, as consistent with a handicap-based explanation (Zahavi 1975).

A second argument rests on the precision with which nanostructures must be arranged for optimal signal expression, and hence their sensitivity to perturbation during development (Ghiradella and Butler 2009). If individuals vary in the stability of environmental conditions (e.g., thermal or nutritional) experienced during development, either incidentally or as the result of active choice, then the resulting signals may act as an index of phenotypic and/or genetic quality (Shawkey et al. 2003; Ghiradella and Butler 2009).

Finally, the accumulating evidence of self-assembly for structural colors (e.g., Prum et al. 2009; Maia et al. 2011), as well as the assumed absence of active and "expensive" cellular processes in the development of nanostructures, has underlain arguments against any expectation of condition-dependence (Prum 2009). This latter assumption appears inconsistent with recent work, however (Rubenstein et al. 2021), and the broader weight of evidence supports the scaling of structural color expression with measures of mate "quality" (reviewed in White 2020), as well as mate choice based on such variation (e.g., Kodric-Brown and Johnson 2002; Kemp 2008a). Though valuable, this body of work remains heavily taxonomically biased toward birds, and more often than not lacks the nonsexual control necessary for tests of heightened condition-dependent expression (Cotton et al. 2004a), thereby limiting the strength of and generality of inferences which may be drawn.

Flies rank among the most diverse animal orders and showcase striking adaptations to support their visually rich lives (Marshall 2012). Relatively poor color vision across the Diptera has historically implied a limited capacity or need for color-mediated communication (Troje 1993), but work in select species continues to document the use of visual ornaments and dynamic displays in the service of mate choice (e.g., Zimmer et al. 2003; Butterworth et al. 2019, 2021). To that end, recent attention has centered on "wing interference patterns" (WIPs) as visual displays and the targets of sexual selection (Katayama et al. 2014; Hawkes et al 2019). These conspicuous patterns adorn the semi-transparent wings of many insects, including flies, and are a product of thin-film interference at the air/chitin interface(s) of wing membranes (Shevtsova et al. 2011). Our understanding of their possible role as signals is nascent, but evidence for their active presentation during courtship (e.g., Frantsevich and Gorb 2006; White et al. 2020), heritability (Hawkes et al 2019), and evolutionary lability in response to sexual selection (Katayama et al. 2014; Hawkes et al. 2019) is consistent with their use as signals, with the encoding of information on mate quality being one plausible, but untested, function.

Lispe cana is a cursorial species of muscid fly endemic to supralittoral habitats spanning the entire Eastern coast of Australia (Pont 2019). They possess sexually dimorphic, structurally colored faces and WIPs, the former of which relatively diffuse reflectors while the latter exhibit limited-view iridescence. These conspicuous patterns are actively presented during distinctive courtship displays in which males pursue females, before engaging in a ritualized ground-based "dance" at close range (Frantsevich and Gorb 2006; White et al. 2020). The clear potential for both male and female assessment during courtship offers a promising context for testing the potential for honesty in structurally colored ornaments, which formed the motivating aim of our study. As discussed below, such colors in holometabolous (completely metamorphic) insects are constructed and fixed during ontogeny from the pool of resources gathered during the larval stage (Rowe and Houle 1996; Hunt 2004). This means that a field sample of adult phenotypes offers a population-level statement of condition and signal expression that effectively integrates all underlying environmental and genetic influences on each. The key prediction for our field-based study, then, was for heightened condition dependence in the structurally colored faces and wings of both male and female *L. cana*, under the hypothesis that such ornaments function as indicators of mate quality.

Materials and Methods

Field sampling

We collected 47 female and 57 male *L. cana* from the supralittoral zone of Toowoon bay, New South Wales, Australia (33.3626°S, 151.4975°E). We humanely euthanized all collected individuals by chill-coma *in situ* using a refrigerated esky, before transporting them to a laboratory at The University of Sydney, Camperdown, Australia, for processing, as described below. We preserved all specimens in a refrigerator at a maximum of 2° to prevent the degradation of structures and/or pigments, and we took all measurements within 3 weeks of capture.

Assessment of condition and color traits

In holometabolous insects, the adult phenotype—including color signals and body size—is constructed from the resources acquired during the larval stage and fixed at eclosion. Since the quality and quantity of larval resources define the "quality" of the resulting phenotype—as closely indicated by adult body size—this total pool of resources can be considered equivalent to individual condition (Rowe and Houle 1996; Hunt 2004). We therefore used adult body size, indicated by thorax length, as a surrogate measure of condition, which is also typical of past work in flies (e.g., Diopsids, David et al. 2000; Cotton et al. 2004b; Neriids, Bonduriansky 2007; Drosophilids, Bonduriansky et al. 2015; and Piophilids, Bonduriansky et al. 2005). We used scaled digital images of collected flies to measure the distance between the anterior prothorax and posterior metathorax in imageJ (Rueden et al. 2017).

To quantify signal expression, we measured the reflectance of 3 body regions across both male and female flies: their structurally colored faces and wings, and their black, melanic abdomens. Abdomens were included as a trait whose visual appearance is assumed to not be under sexual selection (given it is unviewable during courtship), which is an important control for testing the heightened condition dependence predicted by indicator models (Cotton et al. 2004a; White 2020). Prior

to measurement we non-destructively separated the heads and wings of flies from the thorax and mounted each region on a ca. 90 × 90 mm square of matte-black card. We used an OceanInsight JAZ spectrometer with pulsed PX-2 Xenon light source, coupled with a 400 µm bifurcated probe to both send and collect light which we oriented at approximately 45° relative to sampling surfaces. We aligned faces and wings with their dorsal and anterior edges nearest the probe, respectively, and rotated each by ca. 1–3° to achieve a point-measure of reflectance at a local maximum, as is commonly employed in the study of limited-view iridescent signals (Kemp 2008a, 2008b; White et al. 2015). Thus, is it not iridescence *per se* which we are capturing (and which requires a considerably more nuanced approach; Gruson et al. 2019a), but rather a measure of peak reflectance which is standardized across individuals and repeatable within individuals. To the latter point, we took all measurements twice with high repeatability (Pearson's $r = 0.83$ across all measurements) and averaged across replicates for analysis. This setup gave a ca. 2–3 mm sampling spot size, contained within a ca. 4 mm illuminated region, which encompassed the frons and vertex of faces and spanned the entirety of the central wing region between the terminus of the subcostal vein on the anterior margin and the anterior cubital vein on the posterior margin. We used a Spectralon WS-1 and the black card upon which flies were mounted as light and dark standards, respectively, and recalibrated between each measurement.

To estimate the chromaticity and luminance of signals as relevant to potential mates, we used a slightly amended form of the dipteran visual model of Troje (1993). We drew on the visual phenotype of the muscid fly *Musca domestica* as the nearest available analog to *L. cana*, and assumed the involvement of R7p, R8p, R7y, and R8y photoreceptors in chromatic processing, and R1-6 in achromatic processing (Hardie 1986; Troje 1993). For chromatic contrasts we estimated receptor quantum catches as the integrated product of stimulus reflectance, an ideal (i.e., flat across the 300–700 nm range) illuminant, and each receptor's sensitivity function, adapted to ambient viewing conditions, before calculating the difference in relative stimulation between R7y-R8y and R7p-R8p receptors; opponency mechanisms which have been validated in several species (Troje 1993; Borst 2014; Lunau 2014; Schnaitmann et al. 2018). These 2 putative opponent channels define the location of a given stimulus in 2-dimensional dipteran colorspace, from which we took the Euclidean distances between a stimulus and the achromatic center as our measure of saturation (or chroma). We estimated luminance as the absolute stimulation of R1-6 receptors, following the estimation of quantum catches as above. Our goal in using a relatively simple colorspace model of this form, as well as these measures of saturation and luminance, was to intuitively assess signal variation with explicit consideration of key, fundamental features of visual processing in *L. cana*. The corollary question of whether such intrasexual variation is discriminable is a compelling one, but existing models designed to inform such questions (e.g., the receptor-noise limited model; Vorobyev and Osorio 1998) are essentially unvalidated among flies, especially in the "noisy" conditions in which courtship takes places in the wild. They can therefore offer no insight into the discriminability, or lack thereof, of sexual signal variation in *L. cana* with the currently available evidence, though this is an area of clear interest for future work. We conducted all spectral processing

and visual modeling in R (v 4.1.0; R Core Team) using the packages "lightr" (v1.1; Gruson et al. 2019b) and "pavo" (v 2.7.0; Maia et al. 2019).

Statistical analysis

We used generalized linear models fit by maximum-likelihood to test the prediction of heightened condition dependence across 6 signaling traits: the chromaticity and luminance of faces, wings, and abdomens. Each trait served as a response, and we specified the interaction between sex and condition (body size) as predictors in all models, with the latter representing the key test of condition-dependence. We specified a Gaussian error distribution with identity link function for all models (thus equivalent to a linear model), and visually confirmed the assumptions of additivity and residual normality. We also standardized all parameter estimates by centering predictors to have a mean of zero and dividing by their standard deviations for ease of comparison and interpretation (Gelman 2008). All statistical analyses were carried out in R (v 4.1.0; R Core team 2020).

Data availability

Data underlying our analyses are available via Zenodo (dx. doi.org/10.5281/zenodo.5565878).

Results

Facial coloration in *L. cana* is strongly sexually dichromatic (Figure 1A) and condition-dependent (Figure 2A,B). The dichromatism stems from males exhibiting considerably brighter faces than females by virtue of their broadband UV-white reflectance. By contrast, the golden-yellow appearance of female faces is characterized by a sigmoidal-type reflectance with an inflection at ca. 520 nm, which underlies their heightened chromaticity when compared with the achromatic faces of males (Table 1). We saw little evidence for dichromatism in WIPs, though this may in part be a consequence of our measuring at whole-wing scales. We also saw little evidence for sexual differences in the angularity of signals (i.e., the measurement geometries required to elicit maximal reflectance) between the sexes. This is therefore unlikely to have contributed to the apparent lack of dichromatism, though a fuller assessment of WIP reflectance was beyond the scope of this study and would be of considerable future interest. The weakly multi-modal reflectance profiles of wings (Figure 1B and Supplementary Figure S2) are a product of the contributions of individual wing panels which vary in thickness and, hence, chromaticity and brightness. That is, the mosaic of conspicuously chromatic panels is relatively achromatic, and sexually monomorphic, at whole-wing scales (but see the "Discussion" section, and Supplementary Figures S1 and S2, for further detail).

We identified significant condition dependence in the faces of both males and females as indicated by the sex by size interaction. It manifested along separate axes in each sex (Table 2). The faces of larger males are more luminant across the 300–700 nm range (Figure 2A), whereas the faces of larger females are characterized by increased chromaticity (Figure 2B). The reciprocal did not hold, hence the interaction, with no apparent relationship between male condition and facial chromaticity, nor female condition and facial luminance. The WIPs of both sexes bore no relationship to body condition along any dimension, nor did their abdomens as our nonsexual control (Figure 2C–F).
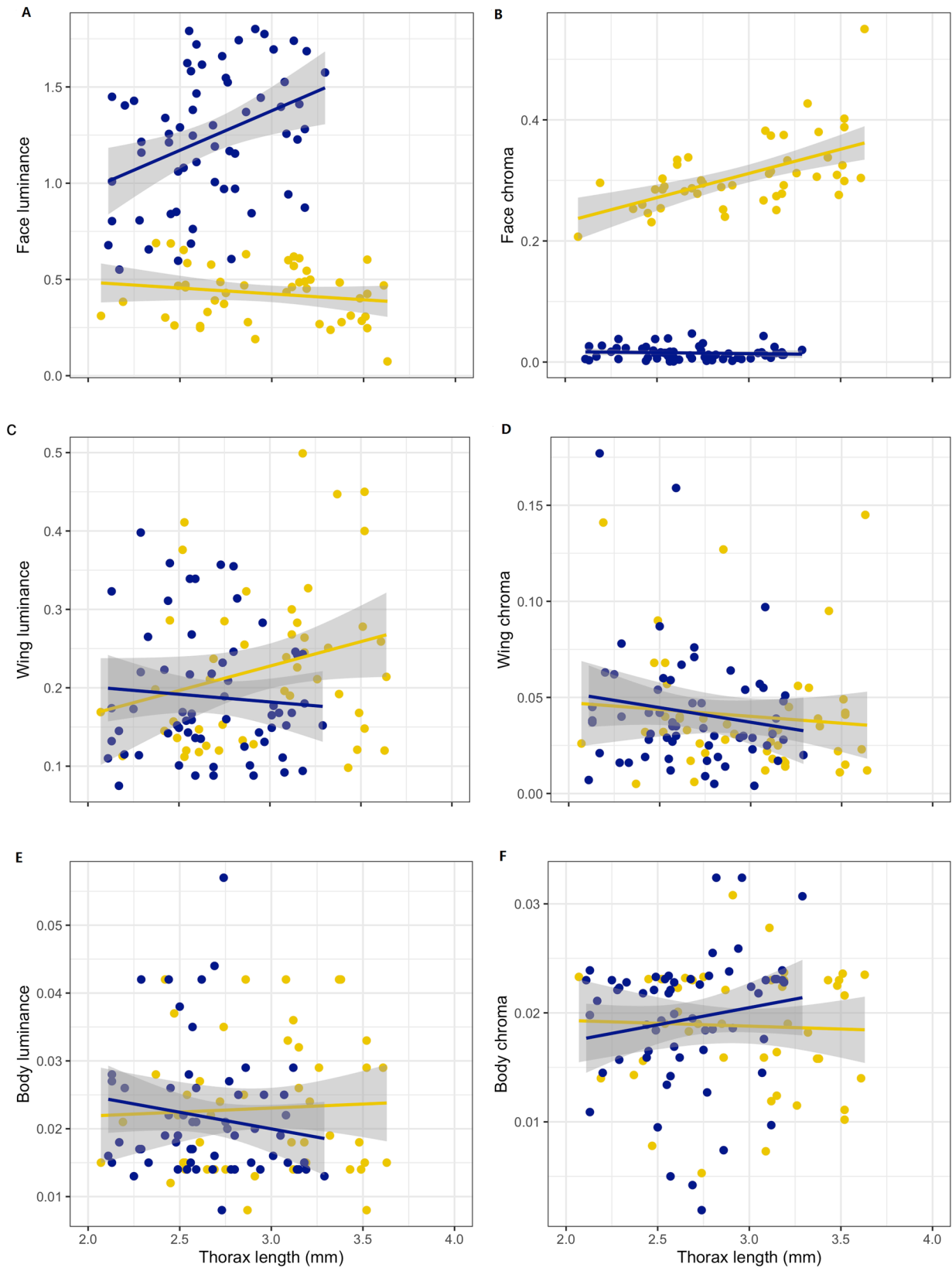
Figure 1. Reflectance spectra (mean ± SD) of the (A) faces, (B) WIPs, and (C) abdomens of male (blue) and female (gold) *L. cana*. Note that males and females are near-completely overlain in (C), and the *y*-axis range varies between plots.

Discussion

Structurally colored ornaments are often-extravagant products of sexual selection, though evidence for their role as

"honest" indicators of mate quality is heterogeneous (White 2020). Here, we examined the key prediction of condition dependence in the structurally colored faces and WIPs of
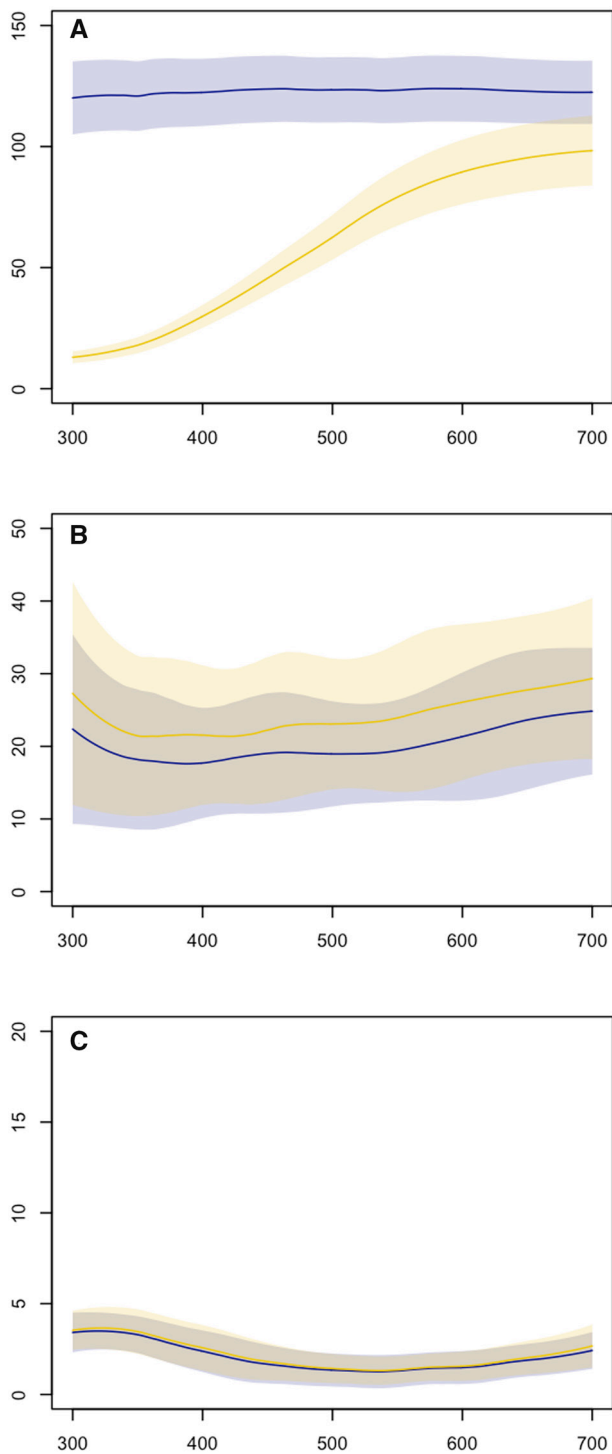
Figure 2. Raw data and linear model fits describing the relationship between color signal expression and individual condition in *L. cana* (*n* = 47 females, 57 males). Shown are estimates of the luminance and chromaticity of the (A, B) faces, (C, D) wings, and (E, F) abdomens against thorax length as a measure of condition, for both male (blue) and female (gold) flies.

the cursorial fly *L. cana*. We found evidence for the moderate to strong scaling of facial signal expression with body size—a proxy measure of condition—in both sexes, albeit along distinct axes. Males in better condition were brighter, while females were more chromatic, and no such relationship was apparent for WIPs in either sex. Comparison against a

nonsexual control supported the contention of heightened condition dependence among these putative signaling traits. Though observational, our results affirm the potential for structurally colored ornaments to serve as informative signals of mate quality, while identifying opportunities for mutual mate choice on complex multi-dimensional ornaments.

The sexual differences we identified in facial coloration and the axes of condition-dependence are underlain by differences in physical mechanisms. The bright UV-white faces of males are the product of incoherent scattering by disordered nanostructures, as is true of non-fluorescent white colors in nature in general (Vukusic et al. 2007; Johnsen 2012; Wiersma 2013). In *L. cana*, the scattering elements are densely packed scales which are modified into flat, elongated bristles (ca. 60 × 6 um) during development (unpublished data; but see Frantsverch and Gorb 2006 for details in closely related species). Although the nanostructural basis of variation within sexes remains to be described, theory (Johnsen 2012) and empirical work (Frantsverch and Gorb 2006) support the primacy of bristle density as a predicted determinant of the among-male variation in facial brightness here identified (Figure 2A), with further possible contributions from bristle geometry and any internal structuring. That is, the sheer number of scattering elements will chiefly distinguish higher from lower quality individuals, and hence the availability and quality of material gathered during the larval stage are a plausible limiting resource. Analogous dynamics are well described in other holometabolous insects, such as the pierid butterfly *Eurema hecabe*. Males display an iridescent ultraviolet wing patch, the brightness of which is driven, in part, by the density of reflective elements adorning individual wing scales (White et al. 2012). The arrangement of these elements is susceptible to perturbation through manipulations of the quality of larval foodplant. Male signal brightness therefore offers a window to juvenile foraging success and developmental environments, which females use to inform their choice of mate (Kemp 2008a, 2008b).

Female facial coloration in *L. cana* shares the same fundamental bristle-based architecture as males, though their golden hue is imparted by the addition of pigments studded across the facial surface. At a proximate level, the condition-dependent variation in saturation we identified (Figure 2B) should be driven by the quantity of underlying pigments and the density of reflective structures acting in concert. More pigments mean a greater fraction of shorter-wavelength incident light will be absorbed, leading to increased spectral purity (Johnsen 2012). Similarly, greater broadband scattering by bristles will increase the relative reflection of longer versus shorter wavelength light, and so will also increase saturation, albeit to a lesser degree.

A mechanistic understanding of the links between female condition and signal expression awaits identification of the pigments in use in *L. cana*, though carotenoids and pterins are likely candidates. The former is dietarily acquired and the latter synthesized *de novo*, and each have been implicated as signals of quality (Weiss et al. 2011). Irrespective of the proximate cause, however, the potential content of such signals is clear in light of the well-recognized scaling of female body size and fecundity in insects (Honěk 1993). Male choosiness is expected to be favored where substantial variance in female quality exists, as suggested here (Figure 2), and when the costs to mate searching and assessment are low (as in the flies' high-density foreshore habits) but mating itself are high

Table 1. Summary descriptors of the visual characteristics of male and female faces and WIPs in *L. cana*

Parameter	Males (*n* = 57)		Females (*n* = 47)	
	Mean	Range	Mean	Range
Facial chroma	0.015 ± 0.001	0.001–0.047	0.308 ± 0.008	0.207–0.550
Facial luminance	1.260 ± 0.045	0.551–1.801	0.427 ± 0.021	0.074–0.689
Wing chroma	0.045 ± 0.005	0.005–0.188	0.041 ± 0.005	0.005–0.019
Wing luminance	0.226 ± 0.022	0.075–0.398	0.226 ± 0.016	0.098–0.499
Abdominal chroma	0.012 ± 0.002	0.002–0.032	0.003 ± 0.001	0.053–0.031
Abdominal luminance	0.022 ± 0.001	0.008–0.057	0.023 ± 0.002	0.008–0.042

Notes: Chroma and luminance were estimated according to a colorspace model considering the visual system of conspecific flies, and abdominal measures are included as a nonsexual control in our tests for heightened condition-dependent expression in signaling traits. Values represent means ± standard errors.

Table 2. Standardized parameter estimates and test statistics from 6 generalized linear models testing for the condition-dependent expression of structural coloration in the faces and wings of the fly *L. cana*

Response	Sex	Condition	Interaction
Facial chroma	**$\beta = -0.28 \pm 0.01$, $t = -40.18$, $P < 0.001$**	**$\beta = 0.02 \pm 0.01$, $t = 3.28$, $P = 0.001$**	**$\beta = -0.06 \pm 0.01$, $t = -4.47$, $P < 0.001$**
Facial luminance	**$\beta = 0.86 \pm 0.06$, $t = 15.47$, $P < 0.001$**	**$\beta = 0.17 \pm 0.06$, $t = 2.88$, $P = 0.005$**	**$\beta = 0.40 \pm 0.11$, $t = 3.46$, $P < 0.001$**
Wing chroma	$\beta = 0.00 \pm 0.01$, $t = 0.24$, $P = 0.810$	$\beta = -0.01 \pm 0.01$, $t = -0.892$, $P = 0.374$	$\beta = -0.00 \pm 0.02$, $t = -0.217$, $P = 0.829$
Wing luminance	$\beta = -0.03 \pm 0.02$, $t = -1.70$, $P = 0.09$	$\beta = 0.01 \pm 0.02$, $t = 0.34$, $P = 0.732$	$\beta = -0.05 \pm 0.04$, $t = -1.44$, $P = 0.154$
Abdominal chroma	$\beta = -0.01 \pm 0.01$, $t = 0.837$, $P = 0.40$	$\beta = 0.01 \pm 0.02$, $t = 1.07$, $P = 0.287$	$\beta = 0.00 \pm 0.01$, $t = 1.08$, $P = 0.281$
Abdominal luminance	$\beta = -0.01 \pm 0.01$, $t = -1.04$, $P = 0.299$	$\beta = 0.00 \pm 0.02$, $t = -1.11$, $P = 0.269$	$\beta = -0.01 \pm 0.03$, $t = -0.90$, $P = 0.370$

Notes: All models included sex (male/female), condition (via thorax length), and their interaction as predictors, specified with a Gaussian error distribution and identity link function. Bolded estimates are statistically significant at $\alpha = 0.05$.

(Bonduriansky 2001). These conditions appear well met in *L. cana*, and males stand to benefit from discriminating among females on the basis of facial saturation, though whether and to what extent they do so remains to be seen.

Unlike faces, we found no evidence for condition dependence among the WIPs of either sex. This is unsurprising among females given their wing patterns are never actively displayed and are unlikely to be incidentally seen by conspecifics. The absence of an effect among males however, for which a signaling role for WIPs is likely, suggests 2 possibilities. One is our measurements did not capture signal variation at the functionally relevant spatial, spectral, or temporal scale. WIPs are a mosaic of panels which are delineated by wing venation. The colors of each element are chiefly defined by the thickness and spacing of the air/cuticle multilayer, as well as any surface structuring such as ridges or bumps (Shevtsova et al. 2011). At whole-wing scales, such as those measured here, the wings of *L. cana* appear to be only weakly chromatic as the contributions of these individual panels average out across the visible spectrum (Figure 1B). Although this represents the experience of most viewers under most conditions, male *L. cana* actively present their wings at a distance of only ca. 5–10 mm during courtship. The visual acuity of *Lispe* is unknown, though data from related species (e.g., minimum resolvable angle of 5° in the muscid *M. domestica*; Land 1997) suggest the possibility that individual wing panels may at least in part be spatially resolvable at these signaler/receiver distances common to courtship (see Supplementary Figure S2 for illustrative example). In which case the appearance of particular wing regions and/or their spatial arrangement may bear salient information on male quality, the signal of which would be masked at whole-wing scales such as those considered here.

By a similar token, males' striking wing patterns are never viewed in stasis. Males rapidly "flutter" their wings during their ritualized courtship dances and move in rapid lateral semi-circles around females who are constantly reorienting in response (White et al. 2020). This presentation behavior suggests a role for the temporal structure of signals as a channel of information. Modifications to the corrugation of wings and/or the arrangement of surface structures (such as microtrichia; Shevtsova et al. 2011) to enhance or suppress limited-view iridescence, for example, may be similarly indicative of resource limitation or broader developmental stress, as discussed above. Yet such variation would only be apparent to us through the measurement of wing signal angularity (which was beyond the scope of the present work), and to conspecific viewers through the active presentation of wings during courtship. There is morphological and behavioral evidence in insects (Kemp et al. 2006; White et al. 2015) and birds (Stavenga et al. 2011) which indirectly supports the possibility, though it remains an intriguing working hypothesis for future study.

The second broad possibility is that WIPs do not function as indicators and instead fulfill one of many other potential roles during signaling. Numerous insects, including flies, are attracted to flashing stimuli (Magnus 1958; Eichorn 2017), with work in butterflies showing this preference can increase linearly up unto the limits of temporal resolution (Magnus 1958). A male's rapidly flickering wings may therefore serve to capture and hold a female's attention during courtship, or bias subsequent gaze directions toward their luminant and centrally located faces.

A second, related, possibility is that male WIPs serve as amplifiers of the true foci of female choice (Hasson 1991; Byers et al. 2010). Their faces are an obvious candidate, though the environmentally contingent nature of WIPs means that the behavioral performance of males during courtship could also be readily assessed. This might, for example, occur through the female assessment of the tempo of male wing-fluttering, as revealed by the flashing of their relatively glossy wings (*sensu* Eichorn 2017). Another consideration is that the limited-view structure of interference patterns displayed on semi-transparent wings means that optimal color expression (or any color expression at all) is only achievable via presentation against suitably dark backgrounds and under sufficiently specular lighting. Male *L. cana* can and do exert some active control over each by biasing the microhabitats in which they display (White and Latty 2020; White et al. 2020). Thus, if a male's ability to select suitable microhabitats varies with some facet of individual quality, then the appearance of WIPs would render such information apparent to female viewers. This would be a novel form of visual signal amplification enabled by direct ties to display environments, though evidence for the broader phenomenon is well established (reviewed in Byers et al. 2010).

Our results support a growing, albeit heterogeneous, body of evidence supporting the potential for honesty among structurally colored ornaments (e.g., McGraw et al. 2002; Kemp 2008b; Griggio et al. 2010;). This was true of both sexes in our focal system which suggests the potential for mutual mate choice, and also extends the male-biased focus in this (White 2020) and related (e.g., Ah-King et al. 2014) areas of research. That we found no evidence for heightened condition dependence in WIPs narrows the scope of explanations for the adaptive evolution of these widespread ornaments (Shevtsova et al. 2011). A complete understanding, however, awaits a richer appreciation of the spectral, spatial, and temporal complexity of WIPs, and color-based signals more generally. Exciting theoretical work continues to advance these aims at several levels (e.g., Stoddard and Osorio 2019; van den Berg et al. 2020), and tractable systems such as *Lispe* sp. hold excellent promise for empirical progress.

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Conflict of interest

The authors no conflicts of interest to declare.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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