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1 **Sexual signals of fish species mimic the spatial statistics of their habitat: evidence for processing** 2 **bias in animal signal evolution**

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10

11

12 **Abstract**

13

14 The diversity of animal visual displays has intrigued scientists for centuries. Sexual selection theory has
15 explained some of this diversity, yet most of this effort has focused on simple aspects of signal design,
16 such as color. The evolution of complex patterns that characterize many sexual displays remains largely
17 unexplained. The field of empirical aesthetics, a subdiscipline of cognitive psychology, has shown that
18 humans are attracted to visual images that match the spatial statistics of natural scenes. We investigated
19 whether applying this result to animals could help explain the diversification of complex sexual signaling
20 patterns. We used Fourier analysis to compare the spatial statistics of body patterning in ten species of
21 darters (*Etheostoma* spp.), a group of freshwater fishes with striking male visual displays, with those of
22 their respective habitats. We found a significant correlation between the spatial statistics of darter patterns
23 and those of their habitats for males, but not for females. Our results suggest that visual characteristics
24 of natural environments can influence the evolution of complex patterns in sexual signals.

25

26 **Introduction**

27 The diversity of visual patterning across animal species remains one of the most striking yet enigmatic
28 of evolution's puzzles. While visual patterns often function as camouflage, or evolve through other
29 modes of natural selection, in many cases they are shaped by sexual selection. Although sexual selection
30 is commonly invoked to explain the exaggeration of a sexual signal (e.g., Andersson 1994), little is
31 known about why particular patterns are selected in some species, while different patterns are selected
32 in others. This question becomes especially perplexing when closely related species exhibit a striking
33 diversity of visual patterns, as in the peacock spiders of Australia, or the manakins of South America.

34

35 Some of the top candidate hypotheses explaining the evolution of signal design are the sensory bias and
36 sensory drive models of sexual selection, which explain how environmental conditions can shape animal
37 sensory systems, and thereby preferences for specific signal features¹⁻⁴. These models have been
38 especially useful for explaining the evolution of simple signal features, such as the color of a visual
39 display, or the frequency spectrum of an auditory signal¹. These features can be interpreted as
40 components of signal efficacy, which refers to a signal's ability to maximize information transmission⁵.
41 In these models, the detectability of a signal determines its attractiveness, hence the central role of signal
42 detection theory in sexual selection research. However, to date, little work addresses the question of how
43 more complex traits, such as intricate visual patterns, can evolve through sensory drive⁶.

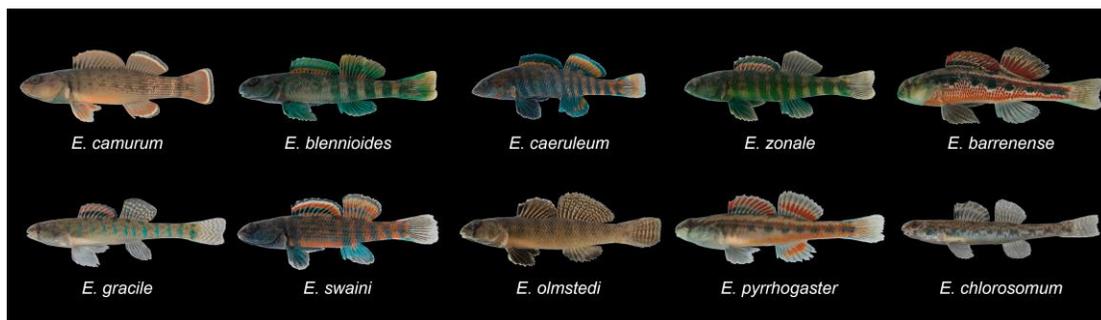
44
45 Recently, Renoult & Mendelson expanded the framework of sensory drive to include efficient
46 information processing as an explanation for complex signal design⁵. Efficiency describes the
47 transmission of information at low metabolic cost. The expanded sensory drive framework posits that the
48 neural circuitry underlying sensory perception is tuned to efficiently process habitat-specific features,
49 and that this specialization can lead to preferences for particular visual patterns, as might be displayed
50 by a potential mate. This hypothesis is grounded in information theory⁷, specifically the efficient
51 processing hypothesis of Horace Barlow⁸. Action potentials are metabolically expensive, and neural
52 systems reduce metabolic expenditure by reducing the number of action potentials required for signal
53 processing⁹. This reduction is accomplished by leveraging the statistical redundancies in sensory stimuli
54 to create a “sparse” neurological representation (or code); that is, for any given stimulus, relatively few
55 neurons are active at any given time, and those active neurons are highly tuned to the redundant (regular)
56 features of the perceptual environment¹⁰. Visual information in particular contains a great deal of
57 statistical redundancy, or regularity, that visual systems have adapted to efficiently process^{11–13}. Similar
58 adaptations for efficiency have also been shown in auditory and olfactory processing^{14,15}.

59
60 The field of human empirical aesthetics uses Barlow's efficient processing hypothesis to explain why
61 humans find certain visual stimuli, like works of art, more appealing than others¹⁶. A number of studies
62 have found that humans prefer, and find more pleasurable, images that are more efficiently processed^{17–}
63 ¹⁹. In parallel, other studies have shown that visual art has fractal-like statistics similar to natural scenes,
64 whereas less aesthetic images, such as those of laboratory objects (i.e. spectrometers, lab benches, etc...) do not.
65 Psychologists hypothesize that people prefer art with the spatial statistics of natural scenes because our brains
66 have evolved to efficiently process them^{20–24}. Results from cognitive psychology therefore suggest a processing bias
67 rooted in the reward (pleasure) of efficient information processing^{5,25}. Renoult & Mendelson hypothesize that
68 this processing bias is not limited to humans, predicting that other animals should also prefer the fractal-like
69 statistics of their habitats, and that this preference could help explain the evolution and diversification of
70 complex animal signal patterns⁵.

71
72 To date, psychological studies of efficient processing have considered natural scenes to be homogeneous,
73 disregarding potential variation between habitats. However, other studies have shown that habitats can
74 differ significantly in spatial statistics, and specifically in the statistics that measure visual
75 redundancies^{26,27}. Such studies quantify the intuitive: an image of the forest understory, with highly
76 repeating vertical contrast (trees), will have different spatial statistics than an image of a desert, or a
77 beach. Thus, organisms occupying habitats with different spatial redundancies are predicted to have
78 environment-dependent differences in visual processing. In keeping with a hypothesis of sensory drive,
79 these processing differences could lead to environment-dependent differences in pattern preferences,
80 with the most efficiently processed (and thus preferred) environments being those inhabited by a given
81 perceiver or by its ancestors. A hypothesis of signal diversification based on processing bias therefore
82 predicts that the spatial statistics of complex visual signals whose function is attraction, as in courtship,
83 will match those of the local habitat⁵. Here, we test that prediction in a diverse genus of freshwater fish
84 with complex visual courtship signals.

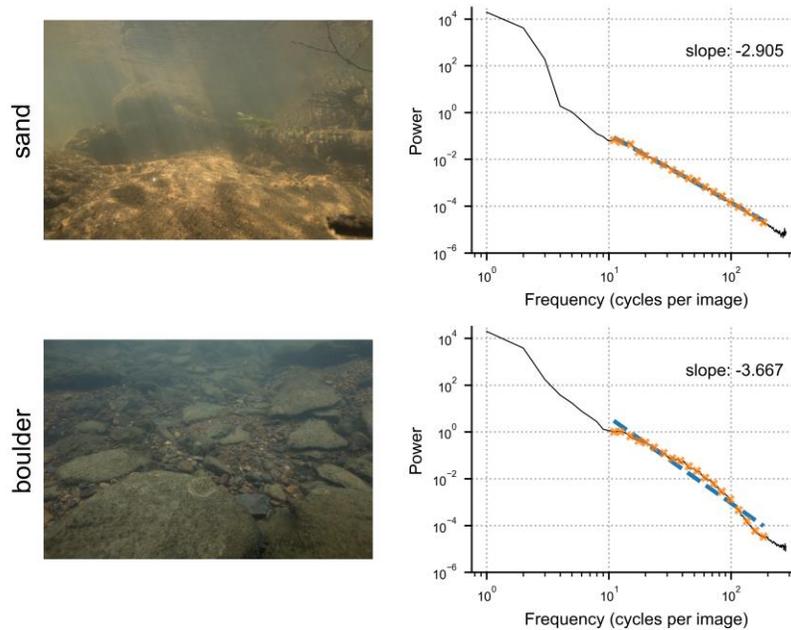
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86 Darters (Percidae: *Etheostoma*) are an especially appropriate system in which to study the diversity of
87 visual patterns in the context of sensory drive and processing bias. Darters are a diverse group of benthic
88 freshwater fish, found throughout the eastern United States²⁸. Phylogenetic evidence suggests that the
89 most recent common ancestor of darters existed between 30 and 40 million years ago, and darters are the
90 second most species rich group of freshwater fish in North America^{29,30}. During their breeding season
91 (typically March through May), male darters of most species exhibit species-specific nuptial coloration
92 used in courtship and competition, while females typically remain drab and cryptic. In addition to their
93 striking male color displays, different species of darters exhibit marked variation in patterning (Figure
94 1). Mate choice assays in some darter species have shown that both males and females prefer the nuptial
95 coloration and pattern of conspecifics^{31–35}. While the most closely related darter species have similar
96 habitat preferences, distantly related species have divergent habitat preferences that distinguish many
97 sympatric species within a community^{36–38}. These distinct habitats could exhibit distinguishable spatial
98 statistics that might drive divergence in pattern preferences and ultimately divergence in the patterns of
99 male sexual signals.
100



101
102 **Figure 1.** Example images for males of each species included in this study.
103

104 In this study, we investigated for the first time whether differences in environmental visual statistics
105 correlate with observable differences in the visual statistics of sexually selected phenotypes. We captured
106 digital images of ten species of darters that occur in five different classes of aquatic habitats, as well as
107 images of their habitats. We used Fourier analysis to characterize the spatial statistics of habitats and the
108 darter species that reside in them and tested for a correspondence between these statistics. Fourier
109 analysis, which decomposes a signal into its component frequencies, is one of the most commonly used
110 methods for analyzing visual images and a central tool in the field of empirical aesthetics^{23,24,39–41}. For
111 visual images, it indicates how luminance contrast (i.e., energy) is distributed across a range of spatial
112 sinusoidal frequencies. Lower spatial frequencies correspond to large scale features in an image, such as
113 the horizon line; higher spatial frequencies correspond to fine scale features, such as grains of sand. When
114 plotted on log-log axes, the relationship between frequency and energy can be approximated by an affine
115 function; the slope of this function is referred to as the slope of the Fourier power spectrum ($1/f$; hereafter,
116 “Fourier slope”; Figure 2). Many studies use the Fourier slope to examine similarities between
117 aesthetically pleasing images and natural scenes^{18,21,42}. We applied these methods to darter color patterns
118 and their preferred habitats, testing a hypothesis of sensory drive.
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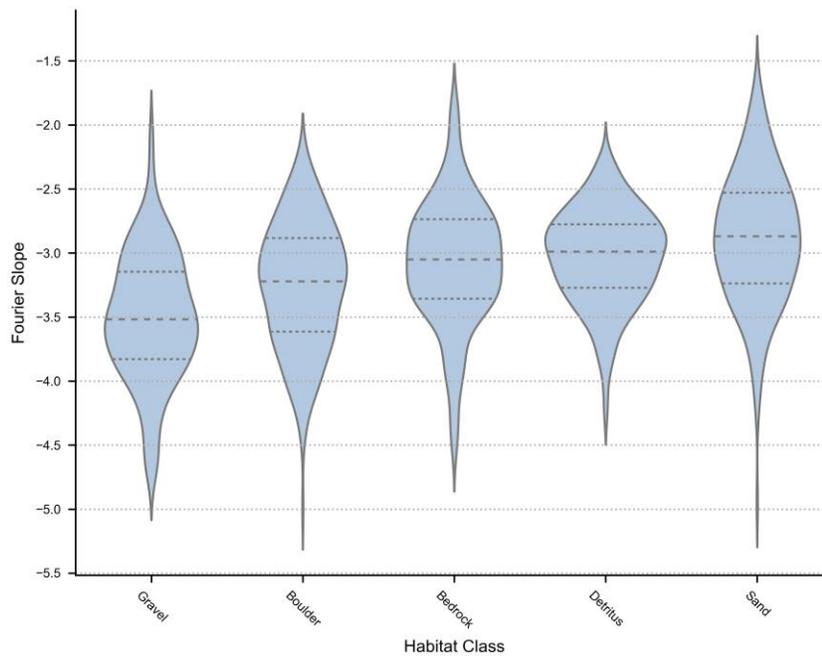
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Figure 2. The Fourier slope of images from two different habitat types. The blue line represents the entire power spectrum, while the orange x's are the bin locations. The black line is the fit of the bins, and represents the slope used for this analysis. For habitat images, the bins are evenly distributed between 10 and 200 cycles per image.

Results

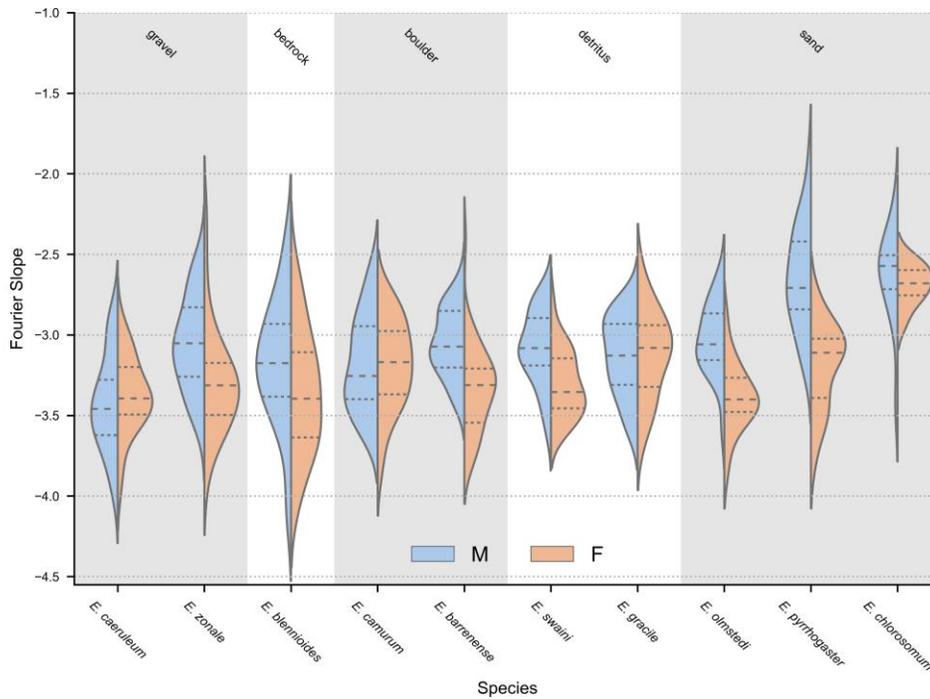
Slope of the Fourier power spectrum

We found significant variation in the Fourier slope across species for both males ($p = 2e-16$, $n = 302$, $F = 16.2$, $df = 9$, Figure 3) and females ($p = 3.47e-9$, $n = 274$, $F = 7.08$, $df = 9$, Figure 3). Overall, males had a higher slope than females (males: -3.09 ± 0.342 SD, females: -3.27 ± 0.306 SD, $n = 576$); this difference was significant in 5 out of 10 species (two-tailed Student's t-test with Bonferroni correction, species' results provided in Supplementary Table 2). Differences in the Fourier slope across habitat classes were also significant ($p = 2e-16$, $n = 2388$, $F = 58.8$, $df = 4$, Figure 4).



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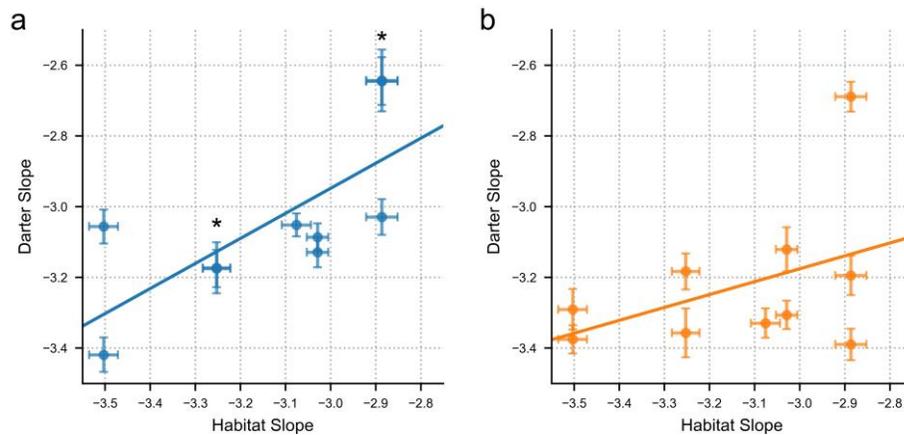
Figure 3. Distribution of Fourier slopes for males and females of ten species in the genus *Etheostoma*. Dashed lines represent the median for each group, and dotted lines represent the interquartile range. The left (blue) half of each violin plot are values for males; the right (orange) half of each violin plot are values for females. Species are grouped by habitat type.



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Figure 4. Distribution of Fourier slopes for images of five habitat types. Dashed lines represent the median for each group, and dotted lines represent the interquartile range.

144 Our model of darter Fourier slopes included habitat slope as a fixed effect, as well as phylogeny and
145 capture site as random effects (models without both random effects had a higher DIC). For the following
146 results, the mean effect size (β) is reported with its 95% credible interval (CI). Results where the CI
147 includes zero indicate a statistically nonsignificant result with $\alpha = 0.05$. The correlation between the
148 Fourier slope of color patterns and that of their corresponding habitat classes was significant for males
149 ($\beta = 0.436$, CI = [0.0442, 0.834], pMCMC = 0.0262, DIC = 60.4, Figure 5a), but not for females ($\beta =$
150 0.295 , CI = [-0.389, 1.03], pMCMC = 0.3709, DIC = 36.72, Figure 5b). We did not find a strong effect
151 of the sample site on the Fourier slope of the fish for either males or females (males: $\beta = 0.0327$, CI =
152 [0.0111, 0.0594], females: $\beta = 0.0323$, CI = [0.0089, 0.0618]). The effect of phylogeny was minimal for
153 males and its exclusion from our model did not change the significance of our results ($\beta = 0.00516$, CI =
154 [1.5e-17, 0.0252]). Additionally, for females the effect of phylogeny was minimal ($\beta = 0.0467$, CI =
155 [0.0023, 0.121]), and its exclusion from our model did not produce a significant correlation between the
156 Fourier slope of females and that of their habitats.
157
158



159
160 **Figure 5.** Scatterplots comparing mean Fourier slopes of fish versus habitat for males (a) and females (b) in ten species of
161 *Etheostoma*. Error bars represent the standard error. For the males, *E. pyrrhogaster* and *E. chlorosomum* have nearly identical
162 values, and appear superimposed on top of each other. This is also the case for *E. camurum* and *E. blennioides*. These species
163 are marked by (*).
164
165

166 Discussion

167 Sensory drive posits that animal signals are shaped by the environments in which they are transmitted^{1,3,4}.
168 Environmental features affect not only signal transmission but also the sensory and perceptual systems
169 of receivers, which in turn can affect the course of signal evolution. Therefore, one of the central
170 predictions of sensory drive is that signals evolving due to sexual selection will vary predictably with the
171 environment in which they evolve³. Our results support this prediction. We have shown that the habitats
172 occupied by different darter species have different visual statistics, measured as the distribution of
173 luminance contrast across different spatial frequencies (i.e., Fourier slope). We also found a significant
174 correlation between the Fourier slope of a species' habitat and that of male nuptial patterns. Our results
175 are therefore consistent with a hypothesis of sensory drive that incorporates efficient information
176 processing in receivers as a driving force in preference and signal evolution⁵.

177

178 The framework established by sensory drive is crucial to our understanding of sexual selection, because
179 it can explain not only why signals become elaborate, but also why they take their particular form^{1,3,4,43}.
180 To date, however, that framework has been rooted primarily in signal detection theory, which does not
181 account for more complex features integrated at higher levels of perceptual processing. In a review of
182 the state of animal coloration research, Endler and Mappes noted that the effect of perceptual processing
183 on the evolution of color patterns is virtually unknown⁶. In addition, of the 154 studies investigating
184 sensory drive analyzed by Cummings and Endler, none leveraged perceptual processing to understand
185 how spatial structure in visual patterns evolve¹. Instead, the bulk of research focused on signal detection
186 via retinal photoreceptors. Information theory is a broader context that motivated the efficient processing
187 hypothesis of Barlow⁸, which emphasizes energy efficiency in information processing. Rooting the
188 framework of sensory drive in information theory thus suggests a novel way forward for understanding
189 how complex sexual signals evolve and a new mechanism through which sensory drive can shape signal
190 design.

191

192 Extending sensory drive to include processing efficiency is motivated by work in empirical aesthetics,
193 which demonstrates that people prefer images that match the spatial statistics of natural (terrestrial)
194 scenes. Much of this work is based on the Fourier slope. Images of terrestrial habitats tend to have a
195 Fourier slope around -2 with surprising regularity. In contrast, images of non-natural items (e.g.,
196 anthropogenic landscapes and objects) have a Fourier slope that deviates from -2^{44,45}. One notable
197 exception is works of art, which tend to have a slope similar to that of natural terrestrial habitats^{20,23,42}.
198 For instance, Redies et al. found that artists' portraits of human faces mimic the Fourier slope of natural
199 landscapes more closely than images of human faces do²¹. Beyond works of art, people also tend to prefer
200 synthetic images with a Fourier slope around -2⁴⁰.

201

202 A preference for Fourier slopes characteristic of natural habitats is thought to arise from the pleasure of
203 efficient processing, as our perceptual systems have evolved to efficiently process the predictable
204 redundancies of the scenes in which we evolved^{11,23,46}. The Fourier slope is a straightforward way of
205 measuring those redundancies and has been shown to correlate with aspects of visual processing. For
206 instance, people are able to discriminate different textures based solely on differences in their Fourier
207 slope²⁶. Moreover, neurons active in the early stages of visual processing in vertebrates are specialized
208 to respond to contrast at specific spatial frequencies. Notably, these specializations correspond to the
209 spatial frequencies that occur with the highest energy in natural scenes^{11,12,47,48}. Stimuli that most closely
210 mimic the energy of spatial frequencies in natural scenes, which is quantified by the Fourier slope, should
211 thus be most efficiently processed, as they generate a sparse neurological code that stimulates a small
212 number of highly specialized neurons¹⁰.

213

214 Although it is now well supported that, in humans at least, efficient information processing is rewarded
215 with pleasure, why this occurs is still unknown^{18,49,50}. One explanation is a “processing bias” (i.e. Renoult
216 & Mendelson)⁵, which supposes that this reward first evolved as an adaptation to inform the brain that
217 information gathering is going smoothly, or that the environment is familiar⁵⁸. Such a processing bias
218 may secondarily be exploited by communication signals that are efficiently processed (e.g., that mimic

219 the visual statistics of a familiar environment) and thereby elicit pleasure⁵. According to this hypothesis,
220 male sexual displays in darters would have exploited female pleasure that originated as a general
221 adaptation not associated with mate choice. Interestingly, we found a correlation between the Fourier
222 slope of darter patterns and that of their habitat only in males, not in females, consistent with a hypothesis
223 that male signals have evolved to be attractive, whereas female signals have not.

224
225 The difference we found between the sexes is puzzling, however, in the context of camouflage, which is
226 the most obvious reason to expect a correspondence between the visual statistics of animal patterns and
227 their environment. If mimicking the Fourier slope of the environment was driven by selection for
228 camouflage, we would expect females, which are also subject to selection by predation, to follow the
229 same pattern as males. Moreover, as males in breeding condition appear to contrast their environment,
230 presumably maximizing detectability to mates or competitors, it seems unlikely that their visual displays
231 are adapted for camouflage. Nevertheless, our analyses consider luminance contrast, rather than
232 chromatic contrast; thus, the luminance patterning of males may be a camouflaged backdrop against
233 which conspicuous colors are displayed. The attention that male colors draw from predators may add
234 increased pressure to be otherwise camouflaged. Although the answer is not yet clear, the interplay of
235 natural and sexual selection in driving the evolution of complex visual patterns remains an open question
236 upon which the spatial statistics of animal patterns and their habitats could be fruitfully brought to bear.

237
238 Last, our finding that variation in the Fourier slope of darters is consistent with variation in species'
239 preferred habitat may have implications for human aesthetics. The Fourier slope has been found to vary
240 between different categories of stimuli (e.g., buildings, natural landscapes, anthropogenic objects), and
241 between terrestrial and aquatic environments (for a review, see Pouli et al.)²⁶; however, the extent to
242 which natural human habitats vary in Fourier slope has not yet been explicitly addressed. Different
243 terrestrial biomes (e.g., tropical forest, desert, seashore) very likely have different Fourier slopes; thus,
244 quantifying how they co-vary with works of art and regional aesthetic preferences may further contribute
245 to understanding the mechanisms driving aspects of cultural evolution and diversification.

246
247 In conclusion, while our study does not directly investigate perceptual processing, it provides a plausible
248 explanation for how sensory integration beyond photoreceptors can drive signal design through an
249 environmentally mediated process. Through the lens of Fourier analysis, we have provided evidence that
250 male visual signals correspond to the visual statistics of their habitats, suggesting that post-retinal visual
251 processing is a plausible explanation for certain aspects of signal design. Our hypothesis is a novel
252 extension of sensory drive, and our methods provide a new approach for testing the role of sensory drive
253 in the evolution of visual patterns. Because the animal patterns we studied are likely used in mate
254 attraction, our results also support key predictions of empirical aesthetics about the relationship between
255 attractiveness and natural scenes. While empirical aesthetics was largely developed to explain human
256 aesthetic preferences, we suggest that some of its principles extend beyond humans and provide a
257 compelling hypothesis for how a complex trait can evolve in a predictable, environmentally dependent
258 direction.

259
260 **Methods**

261 **Darter Collection and Photography**

262 We collected males and females of ten darter species from 23 sites distributed in Illinois, Kentucky,
263 Maryland, Missouri, Pennsylvania, and Tennessee (*Etheostoma barrenense*, *E. blennioides*, *E.*
264 *caeruleum*, *E. camurum*, *E. chlorosomum*, *E. gracile*, *E. olmstedii*, *E. pyrrhogaster*, *E. swaini*, *E. zonale*)
265 (Supplementary Table 1). These ten species were chosen for inclusion based on their broad phylogenetic
266 distribution and their preference for different classes of habitat: sand (*E. chlorosomum*, *E. olmstedii*,
267 *E. pyrrhogaster*), boulder (*E. blennioides*, *E. camurum*), gravel (*E. caeruleum*, *E. zonale*), detritus (*E.*
268 *gracile*, *E. swaini*) and bedrock (*E. barrenense*). At each site, we collected approximately 10 males and
269 10 females (males: 11.2 +/- 3.0 SD; females: 10.5 +/- 3.1 SD), which were subsequently photographed.
270 Darters were caught by kick-seining and brought back to either the Hancock Biological Station in Murray,
271 KY or University of Maryland Baltimore County. Fish were housed in aerated tanks and photographed
272 within three days of capture. Immediately prior to photography, fish were euthanized in MS-222 and then
273 fixed in 10% formalin with fins pinned erect for approximately 10 minutes. We then clipped the pectoral
274 fin of each fish for an unobstructed image of their body pattern. Images were subsequently captured with
275 a Canon EOS 5D Mark IV digital camera mounted to a Cognisys Stackshot system to ensure a fully
276 focused image (see Supplementary Information for detailed photography methods).

277

278 **Habitat Photography**

279 We collected images of habitats at sites where we captured darters using an Ikelite 200DL underwater
280 housing for a Canon EOS 5D Mark IV digital camera. Each darter species was assigned to a habitat class
281 (sand, gravel, boulder, detritus, or bedrock) based on where darters were observed, as well as on literature
282 describing darter microhabitat preferences⁵²⁻⁵⁴. Each habitat class was represented by a minimum of 100
283 images representing a minimum of two sites. All images were collected in clear, shallow water on sunny
284 days between 10:00 and 15:00, and when water turbidity was low (see supplementary information).

285

286 **Image Conversion to Darter Color Space**

287 For all images, RAW files were converted to 16-bit tiff files using the rawpy python API. We converted
288 RAW files to RGB triplets without any spatial interpolation, gamma correction or white-balance to
289 maintain linearity. Images were then converted into a darter colorspace. The generation of the darter
290 colorspace was done by first characterizing the sensitivity functions of our camera, and then using known
291 darter visual sensitivities to generate a mapping from camera space to darter space⁵⁵. The sensitivity
292 functions for the camera were estimated using a monochromator and a calibrated spectrometer, which
293 ensured that each color channel was linear⁵⁶. To model darter color vision, we generated a dichromatic
294 model using cone sensitivities peaking at 525nm and 603nm (darters lack a short wavelength sensitive
295 cone class). Since the cone sensitivities for all species in this study are not currently known, we used the
296 same color vision model for all species. Variation between darter species in cone sensitivities is known
297 to be relatively minor and unlikely to affect the outcome of our analysis⁵⁵. We converted camera space
298 to darter space by minimizing the difference between the camera model and the cone model, using a
299 second order polynomial function of RGB values. We then converted all images (fish and habitat) from
300 color space to luminance space by summing the two color channels. This pooling of color channels
301 closely mimics how vertebrate brains are thought to extract luminance information⁵⁷.

302

303 For darter images, we cropped out the region on the flank of each fish directly below the second dorsal
304 fin. From the set of cropped images, we determined the largest square area that would fit in every cropped
305 image, which was found to be 200 x 200 pixels. For each darter image, we then randomly sampled a
306 region of this size from the flank of the fish. Habitat images were reduced from their original dimensions
307 of 2251 x 3372 to 800 x 1200. We then randomly sampled each habitat image four times with a 400 x
308 400 pixel square. Since the size of the habitat images is greater than the size of the darter's flank, using
309 a larger box size reduces variability in lower frequency coefficients. Additionally, we tested the effects
310 of various box sizes, and found our results robust to these changes (see supplemental information).

311

312 **Fourier Analysis**

313 To compute the slope of the Fourier power spectrum for each image, we followed standard methods in
314 empirical aesthetics^{21,42,58}. We calculated the two-dimensional Fast Fourier Transform with a Kaiser-
315 Bessel window using parameter $\alpha = 2$ to minimize edge artifacts²⁶. We then transformed the Fourier space
316 to the power spectrum and estimated the radial average of the power spectrum. To eliminate edge effects
317 and high frequency noise, we only included spatial frequencies between 10 and 110 cycles per image.
318 Since the Fourier power spectrum has a greater spatial granularity at higher frequencies, we binned each
319 power spectrum between 10 and 110 cycles for darter images and between 10 and 200 cycles for habitat
320 images, with 20 bins for each. This ensures that our slopes were calculated to give equal weight across
321 the frequency range. We then estimated the slope of the power spectrum using a linear regression on the
322 bin values, using a custom Python script.

323

324 **Statistical Analysis**

325 To ensure that images of species-typical habitat were representative of their class, we pooled images of
326 each habitat class across multiple sites. We then compared the Fourier slope across habitat classes and
327 across darter species (males and females analyzed separately) using ANOVAs. To examine the
328 relationship between the Fourier slope of habitats and that of darter patterns, we used generalized linear
329 mixed models. We computed this model using the R package MCMCglmm^{59,60}. Our model predicted the
330 value of the Fourier slope of each individual fish based on the slope of their habitat. Capture site and
331 phylogeny were included as random effects. The phylogenetic tree of the ten studied species was inferred
332 from a previously published molecular phylogeny (accessed via TreeBASE)^{30,61}. We ran the model using
333 the uninformative Inverse-Wishart prior for 1,000,000 iterations, with a 10,000 iteration burn in and 50
334 iteration thinning.

335

336

337 **Data Availability**

338 All code used to compute the slope of the Fourier power spectrum can be accessed via github at
339 <https://github.com/svhulse/Fourier-Analysis>. The computed slopes for every image used can also be
340 accessed via github under the same repository. Any images used in this study are available upon
341 request.

342

343

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473 **Author contributions**

474 T.C.M. and J.P.R. conceived and designed this study. S.V.H. collected fish with assistance from T.C.M.
475 and J.P.R., and was responsible for all photography. Additionally, S.V.H. wrote all python code and
476 performed all analyses. All authors worked to write and edit the manuscript.

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479 **Competing interests**

480 The authors declare no competing interests.

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483 **Materials & Correspondence**

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E. camurum



E. blennioides



E. caeruleum



E. zonale



E. barrenense



E. gracile



E. swaini



E. olmstedii

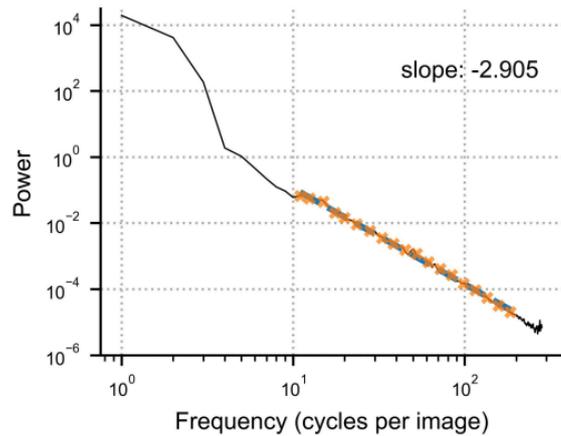


E. pyrrhogaster

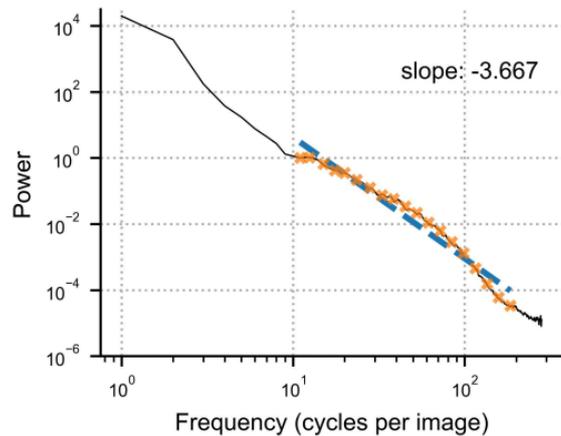


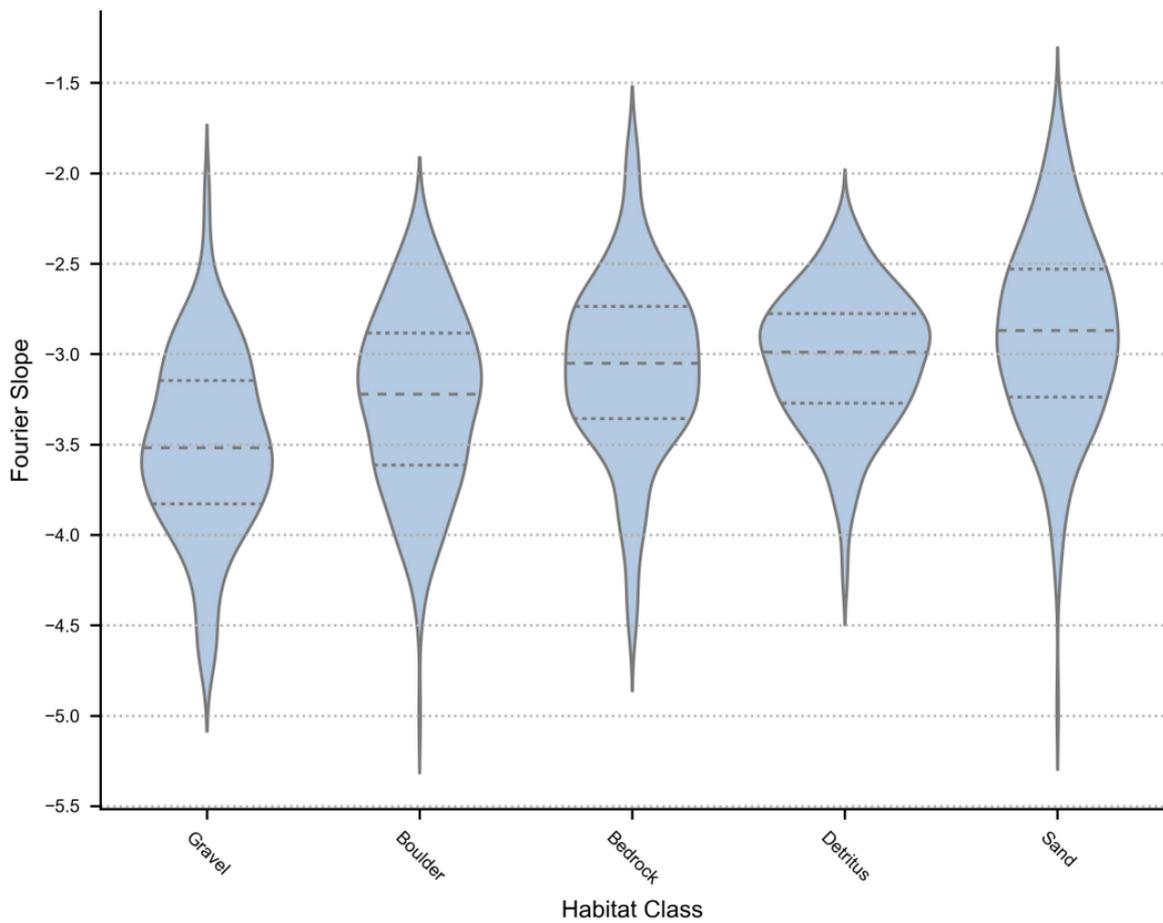
E. chlorosomum

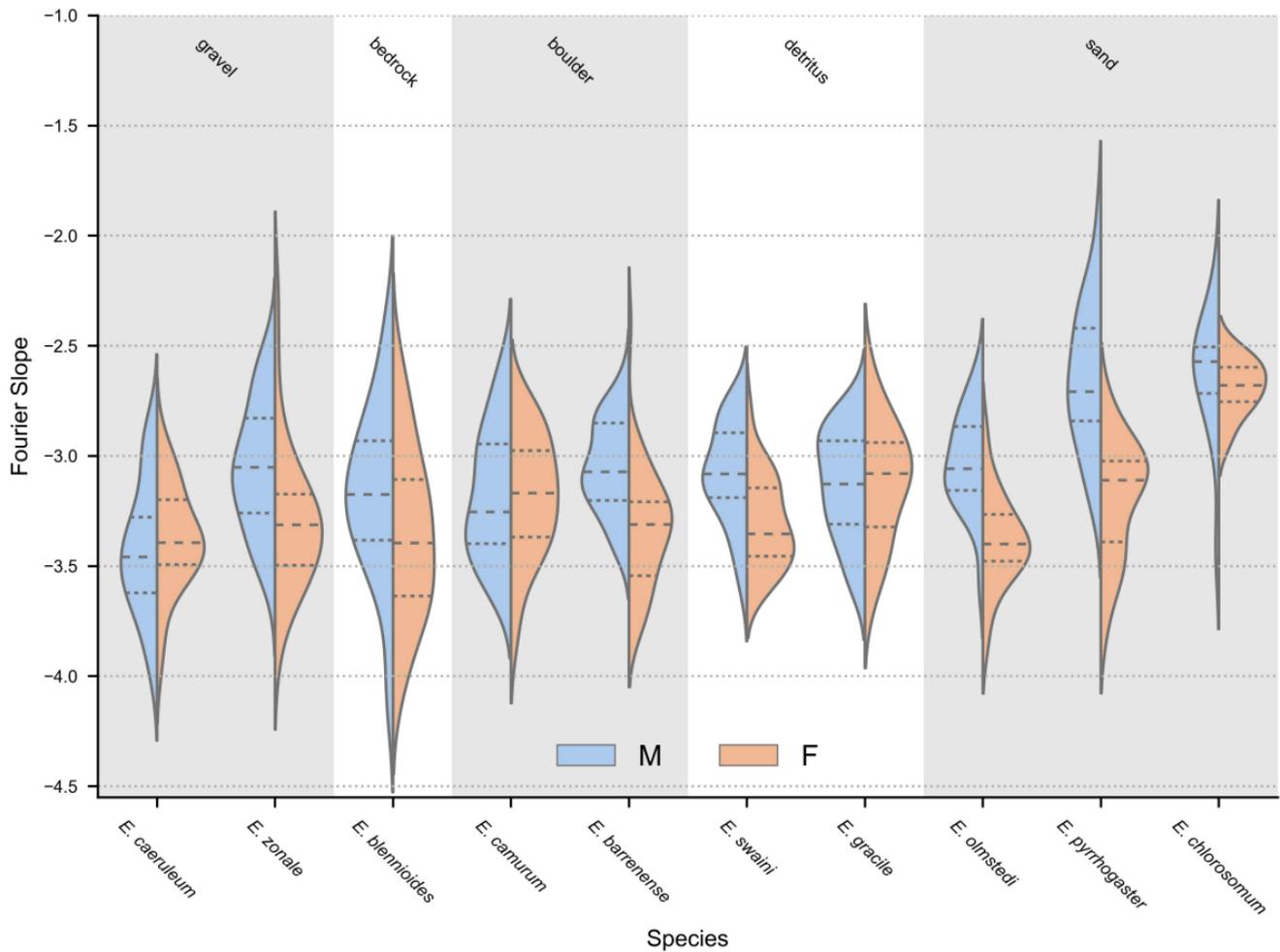
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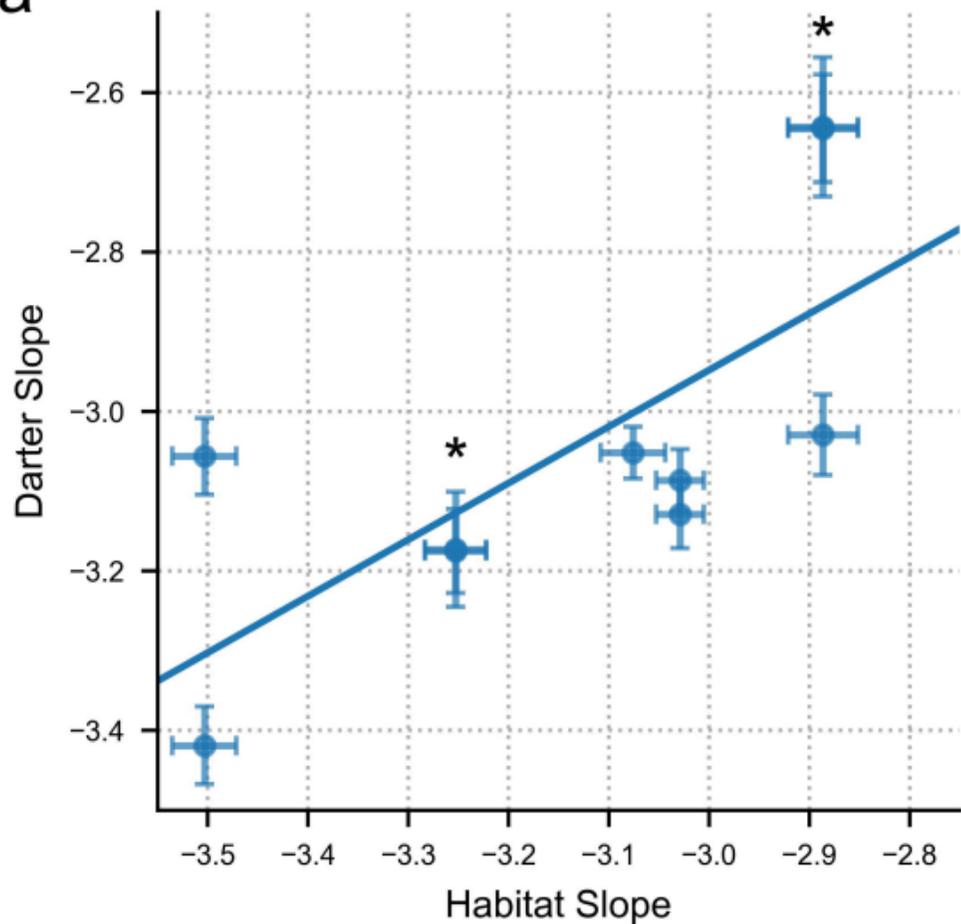


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