Functional Integration of Multiple Sexual Ornaments: Signal Coherence and Sexual Selection

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ABSTRACT: The sexual ornamentation of animals typically consists of multiple distinct traits. The classical research approach focuses on differences among these traits, but this approach may often be misleading because of correlations among distinct sexual traits of similar origins. There are many published studies on the correlation structures of sexual traits, but the way receivers take into account the components of an integrated, multicomponent trait system remains mostly unknown. Here, we propose a general analytical framework to assess the possible sexual selection consequences of within-individual coherence in the expression of multiple correlated sexual traits. We then apply this framework to a long-term mutual plumage coloration data set from a wild bird population. The results suggest that the coherence of component plumage color traits is not sexually selected. However, component trait coherence affects sexual selection on integrated plumage color. When assessing across-spectrum plumage reflectance, receivers choosing mates apparently disregard a component trait if it is inconsistent with the overall expression of other components. This indicates that separately examining and manipulating distinct sexual traits may often be misleading. Theoretical and empirical studies should further explore the effects of coherence on the ornament-preference coevolution.

Keywords: backup signals, plumage color, signal deterioration, systems approach.

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genic capture (Cooperman et al. 2007; Johnston et al. 2013) or shared hormonal regulation (Blas et al. 2006). Studies of how correlated sexual traits evolve and work are gradually accumulating. Several studies concentrate on the changes of correlation structure and trait function assignment (Garamszegi et al. 2006; Wilkins et al. 2015; Rosenthal et al. 2018; Cronin et al. 2019), while others examine the determinants, mechanisms, and consequences of integration (Badyaev et al. 2001; Abbott and Svensson 2008; Higginson et al. 2016; Levin et al. 2018). However, widespread research on the “phenotypic integration of sexual ornamentation” has paid little attention to functional integration (i.e., how the integrated trait complex is processed at the individual level and how receivers handle the expression of “component” traits). From an evolutionary perspective, it has been suggested long ago that receivers may benefit by integrating information from multiple correlated sexual traits (or repetitions of the same trait) to obtain an overall, more reliable picture of the signaler (Johnstone and Grafen 1992; Krakauer and Johnstone 1995; Smith and Evans 2013; Lengagne et al. 2017). Recent reviews and opinion papers have also repeatedly proposed

Table 1: Literature evidence for correlation among distinct ornamental traits

| Species                  | Type | Reference                              |
|--------------------------|------|----------------------------------------|
| Aethia pusilla           | 1    | Jones and Montgomerie 1992             |
| Aptenodytes patagonicus  | 0    | Viblanc et al. 2016                   |
| Calamospiza melanocorys  | 1    | Chaine and Lyon 2015                  |
| Callipepla californica   | (1)  | Calkins and Burley 2003               |
| Cardinalis cardinalis    | 2    | Jawor et al. 2004                     |
| Colaptes auratus         | 0b   | Wiebe and Vitousek 2015               |
| Coracias garrulus       | 1    | Silva et al. 2008                     |
| Cyanistes caeruleus      | 1, 3 | Ferrer et al. 2015                    |
| Drosophila biceptinata   | 3    | Cooperman et al. 2007                 |
| Drosophila hunnanda      | 1    | Van Homrigh et al. 2007               |
| Euplectes ardens         | 1c   | Andersson et al. 2002                 |
| Falco tinunculus         | 1    | Vergara and Fargallo 2011             |
| Ficedula albicollis      | 1    | Laczi et al. 2011                     |
| Ficedula hypoleuca       | 0    | López-Arrabé et al. 2014              |
| Geothlypis trichas       | 1, 3 | Taff et al. 2012                      |
| Hirundo rustica          | 1    | Hasegawa et al. 2010                  |
| Malurus cyaneus          | 0    | Mahr et al. 2016                      |
| Pachycephala pectoralis  | 1, 3 | Van Dongen and Mulder 2009            |
| Parus major              | 1    | Hegyi et al. 2015                     |
| Passer domesticus        | 1    | Laucht and Dale 2012                  |
| Phasianus colchicus      | 1, 2 | Rubolini et al. 2006                  |
| Plectrophenax nivalis    | 1    | Guindre-Parker et al. 2013            |
| Psamophillus dorsalis    | 1    | Deodhar and Isvaran 2018              |
| Ptilonorhynchus violaceus| (1, 2)| Doucet and Montgomerie 2003         |
| Rhamphomyia longicauda   | 1    | Wheeler et al. 2012                   |
| Schizocosa floridana     | 1    | Rosenthal et al. 2018                 |
| Setophaga cerulea        | 1    | Boves et al. 2014                     |
| Setophaga petechia       | 1    | Grunst et al. 2014                    |
| Stagonopleura guttata    | 3    | Zanollo et al. 2013                   |
| Sula dactylatra          | 2    | López-Rull et al. 2016                |
| Tragelaphus oryx         | 3    | Bro-Jørgensen and Beeston 2015        |
| Turdus migratorius       | (1)  | Row and Weatherhead 2011              |
| Zonotrichia atricapilla   | 1    | Chaine et al. 2011                    |

Note: The list is certainly not exhaustive, and it does not constitute a proper meta-analysis. It does show, however, that correlation among distinct ornamental traits is present in most of the examined species. “Type” refers to trait pair types that were found to be correlated and is coded in the following way: 0, no correlation was detected among the distinct sexual traits examined; 1, traits of the same modality and similar temporal variability were correlated; 2, traits of the same modality but different temporal variability were correlated; 3, traits of different modality were correlated.

- Small sample size, nonsignificant correlations with effect size $\geq 0.3$ were counted as correlations.
- Only $P$ value is given.
- Negative correlation.
- Correlations were partly negative and changed because of prenatal hormone treatment.
the unstudied possibility that receivers may form a single percept from multiple sexual traits (Prokop and Droboniak 2016; Pérez-Rodriguez et al. 2017; Halfwerk et al. 2019; Mitoyen et al. 2019), and this would certainly involve functional signal integration (i.e., treating the whole integrated trait complex as a single signal [hereafter, “integrated signal”] and the individual traits as signal components).

The first step toward understanding the integrated functioning of sexual traits is to test whether functional integration is present at all, and such tests are scarce in natural populations (Poole and Murphy 2007; Laczi et al. 2011; Hegyi et al. 2015; Lengagne et al. 2017). This is unfortunate, principally because widespread presence of functional integration among sexual traits would necessitate paradigm shifts and methodological changes in our studies of complex sexual ornamentation; we can no longer interpret the expression of component traits independently, and manipulations of any sexual trait should take into account the expression of other correlated traits. Many further questions also arise concerning integrated signals—for example, how the strength of component trait interrelation depends on the environment or on individual trait deterioration, how the strength of interrelation affects the strength of sexual selection on the integrated signal, and how receivers deal with outlying trait expression values (e.g., one trait that is extremely highly expressed while the others are generally poorly).

**Sexual Signal Coherence: Definition, Measurement, and Importance**

Studying the integrated functioning of sexual traits necessitates the quantification of their coherence. We can define signal coherence as some measure of the consistency of the expression of component traits at the individual level, and we can define incoherence as an individual-level measure of signal inconsistency. As a rough example, signal expression of an individual in which all component traits are highly expressed (relative to their population means) can be considered coherent. Signal expression of another individual with high expression of some traits and low expression of other traits is then considered incoherent. One way to quantify incoherence in an integrated signal is to bring the expression of component traits to a common scale (e.g., by standardization), estimate integrated signal expression specific to the individual by averaging these standardized values across traits (hereafter, “individual-specific mean”), and calculate the deviations of component trait expression values from this individual-specific mean.

Indirect evidence suggests that the ability or even tendency to evaluate aspects of signal coherence may be widespread in multiple ornament systems. Results suggesting this include, for example, (1) selective attention to more reliable stimuli among multiple available stimuli (Rubi and Stephens 2016), (2) evaluation of a given sexual trait in the light of other traits (use of trait composites [Burley et al. 2018], hierarchical trait use [Murray et al. 2018]), (3) perceptual grouping of elements of sensory input according to their similarity in simple attributes (feature binding; Miller and Bee 2012), (4) preference for consistency among repeated renderings of a single sexual trait (Byers 2007; Botero et al. 2009; Byers et al. 2010; Rivera-Gutierrez et al. 2011), and (5) strong effects of extreme outlying values on preference at such repeated sexual trait production (Clemens et al. 2014; Reichert et al. 2017). However, how receivers deal with individual incoherence and outlying values in multiple different components of an integrated sexual signal is, to the best of our knowledge, unknown.

In natural populations, signal coherence assessment is unlikely in systems with correlation structures that are strongly environment dependent, where correlated sexual traits will probably function as independent signals (Chaine and Lyon 2015; Rosenthal et al. 2018). It is most likely to occur among multiple sexual traits that have the same modality and therefore a similar scale of temporal variability (the situation is more complicated across modalities; Henderson et al. 2018; Ferrer et al. 2021). Unimodal systems of correlated sexual traits apparently represent the most frequently encountered scenario in the literature (table 1), so signal coherence assessment may be the norm rather than the exception in sexual signaling. The most widely studied unimodal signal system consists of color traits. Typically, more than one color trait is present in the same species (Chen et al. 2013; Delhey and Peters 2017), and these may also show characteristic patterns of parallel change and covariation (Grunst et al. 2014; Hegyi et al. 2015; Robinson and Gifford 2018). However, there are less widely examined but similarly likely targets for signal coherence assessment, such as song characteristics (Garamszegi et al. 2006), sexually selected chemical blends (Nielsen and Holman 2012), and courtship display repertoires (Deodhar and Ivaran 2018).

We argue that signal coherence of the individual may play a crucial role in the assessment process and may also have important evolutionary consequences and practical relevance for studies of correlated sexual traits. For example, if the expression of correlated traits is pooled by the receiver regardless of the degree of its coherence (i.e., a single attractiveness value is derived from all traits), this pooling may simply reduce the power of empirical studies focusing on individual traits. If, however, the processing of correlated traits involves an assessment of the degree of component coherence, this may radically confound studies of the function and information content of individual sexual traits.
**System-Level versus Traitwise Incoherence and Possible Responses by Receivers**

Two possible sources of incoherence may produce different distributions of component trait expression around the mean and may lead to different signal processing strategies by the receivers (fig. 1). One source of incoherence may be consistent differences among individuals in developmental stability (i.e., ability to regulate the expression of their sexual traits or adjust it to their physiological state; Klingenberg 2019). In such a case, no single component trait value will dominate as the greatest cause of signal incoherence, and we will see a continuous distribution of incoherence, a situation we may call “system-level incoherence” (left side of fig. 1). The second source of component trait incoherence is “damage” specific to the expression of one component trait (e.g., developmental abnormality or soiling restricted to a given ornamental plumage area), resulting in an outlying component value but leaving the expression of other components intact. This could be termed “traitwise incoherence” (right side of fig. 1). In any natural signal system, traitwise and system-level incoherence are expected to be simultaneously present.

An adaptive response of receivers to traitwise incoherence may be to omit the outlying component value from the integrated signal calculation (signal filtering). If the components are developmentally integrated and the outlier is a “damaged” component, then its omission may lead to a better approximation of the “original,” undamaged expression of the integrated signal and therefore individual quality (fig. 2). Sensory, cognitive, or environmental differences will likely lead to individual variation in the filtering threshold (Ronald et al. 2012; see, e.g., Chavez et al. 2014), but there will be a threshold above which most or all individuals will filter the outlying signal component. By contrast, in cases of system-level incoherence, signal coherence may be partly independent of overall trait expression and may therefore itself be subject to sexual selection. That is, receivers may prefer individuals with more coherent signal expression in addition to higher signal expression. Importantly, the processing strategies of receivers may not match the prevalent type of incoherence but rather reflect constraints in their signal processing system. For example, passive cognitive mechanisms (e.g., feature binding; Miller and Bee 2012) may lead to signal filtering even in cases with substantial system-level variation in incoherence. To the best of our knowledge, no study of integrated sexual trait systems has explicitly examined either sexual signal filtering or sexual selection on signal coherence.

**Analyzing Coherence Effects on Sexual Selection**

How can we detect the effects of signal incoherence on sexual selection? We suggest that such effects may be readily testable on quantitative measures of sexual selection based on the natural variation of sexual traits in nonmanipulated individuals. Such quantitative measures

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**Figure 1:** Illustration of the two types of incoherence in the expression of correlated sexual traits. Each symbol represents the expression value of a single component trait along a standardized axis (all traits on the same scale, relative to their population means). In the middle, an individual with low incoherence can be seen. One of the two types of incoherence increases with the distance from this individual, as indicated by the arrows.
include, for example, correlations between sexual trait expression and preference in no-choice mate preference tests, correlations of mating success or mating latency with sexual trait expression, and assortative mating when the sexual trait system is qualitatively identical in the two sexes. Below, we detail a possible analytical approach and then apply it to a field data set. As one of the above sexual selection measures should fit to almost any study system, the analytical approach detailed below should also be broadly applicable.

To look for sexual selection on coherence, we may simply repeat the same correlative test of sexual selection (mate preference, mating success, mating latency, assortative mating) but replace integrated signal expression by a quantitative measure of signal incoherence (e.g., the standard deviation of standardized component trait expression data at the individual level). In the above examples, tests should indicate, respectively, preference, increased mating success and reduced mating latency for more coherent individuals, and assortative mating for coherence. If our sexual selection measure is relevant, lack of a robust pattern in such a test will strongly argue against sexual selection on coherence.

To detect signal filtering, we may impose an artificial filtering gradient (i.e., multiple filtering steps along a series of thresholds) on the component trait data and look at the resulting changes of sexual selection estimates in the data sets subjected to filtering to see whether these changes are consistent with natural signal filtering. The logic of this exercise is the following. If receivers filter component trait expression, the outlying component trait values are not taken into account at mate choice. Accordingly, our estimates of sexual selection should improve after artificial filtering of the “raw” component trait values. We must note in advance that this approach is not testing sexual selection at the population level but applies such estimation only in the context of the filtering exercise. In the exercise, sexual selection is tested in each filtered subsample before and after the filtering. Therefore, the term “sexual selection estimate” as used in the filtering exercise should not be viewed as an estimate of selection on the focal trait in the population. It is simply a response variable in the exercise.

The artificial filtering (illustrated by fig. 3) begins with finding the most deviant component trait value for each individual (e.g., the trait value that deviates most from the individual-specific mean of the standardized component traits). We then specify a gradient of artificial filtering thresholds above which we will consider the most deviant component value an outlier and select and analyze the subsamples of data in which the most deviant component value exceeds the given threshold. Increase of the outlier detection threshold toward more permissive values will gradually reduce the number of individuals in these samples as fewer and fewer outlying values and therefore individuals qualify for exclusion (see fig. 3). The highest (most permissive) threshold should therefore be a value that still applies to a sufficient number of individuals to allow a quantitative test of sexual selection on this sample. The lowest (most stringent) threshold, on the other hand, can be a conventional deviation value for an outlier (e.g.,

Figure 2: Hypothetical example of signal filtering on the expression of correlated sexual traits by receivers. The standardized expression (same scale, relative to population mean) of five component traits is shown in four individuals (A–D). The open circles refer to undamaged traits. The filled circles represent the outlying expression value of a damaged component trait (a case of traitwise incoherence). Horizontal lines indicate overall trait expression estimates from all components (unfiltered, black lines) and without the outlier (filtered, gray lines).
We also have to specify a meaningful number of intermediate thresholds between the lowest and the highest threshold value to quantify the detailed pattern of filtering effects. In the final part of the exercise, we take the series of subsamples that contain individuals with outliers using the given series of selection criteria. For each subsample, we calculate a prefiltering sexual selection estimate based on the raw trait expression data. Then for each individual of a given subsample, we remove the outlying component trait value and recalculate integrated signal expression of the individual without the outlier (as in fig. 2). We finally recalculate our sexual selection measure in the subsample using the outlier-filtered data of integrated signal expression. This analysis yields a series of original and "filtered" sexual selection estimates (one pair for each subsample), which we can then examine as a function of the artificial filtering threshold. We need to analyze sexual selection before and after the filtering for each subsample to (1) correct for inherent, systematic differences among subsamples and (2) remove the error and possible bias introduced by including the whole unfiltered population in each analysis. Such error and bias would very likely weaken, distort, or swamp the meaningful patterns produced by the filtering exercise (see more details in "Material and Methods").

Three scenarios with distinct predictions can be envisioned, as illustrated in figure 4. Under the first scenario, receivers use signal filtering. We assume that this filtering is characterized by a single general threshold value, although this may vary slightly among or even within individuals. If we do the artificial filtering using a given threshold value, we may filter two types of data. On the one hand, there may be individuals that are below the natural threshold and are therefore not filtered by the receivers. Artificially filtering the outlying component values of these individuals may reduce the sexual selection estimate. On the other hand, there may be individuals that exceed the natural threshold and are therefore filtered by the receivers. Artificially filtering the outlying component values of these individuals may reduce the sexual selection estimate. On the other hand, there may be individuals that exceed the natural threshold and are therefore filtered by the receivers. Artificially filtering the outlying component values of these individuals decreases the sexual selection estimate. The proportion of the two types of individuals changes in the sample depending on the position of our artificial threshold relative to the natural threshold, and we expect this to produce a characteristic response curve shape in the change of our sexual selection estimate compared with the nonfiltered state (solid line in fig. 4). Overall, we expect that the change of the sexual selection estimate will be positive. Moreover, we expect that the increase will initially be strongly accelerating but then the magnitude of this acceleration will drop after reaching the natural filtering threshold. In the
affected samples are naturally 
with the threshold (shown by A), most individuals in the affected sam-
subsamples, when assuming three different scenarios: when there is 
degradation between our measurements (dotted line), and when there is 
neither degradation nor filtering (dashed line). Note the position of 
the origin on the y-axis. The capital letters indicate stages where the propor-
tion of individuals subjected to natural filtering still increases steeply 
with the threshold (shown by A), most individuals in the affected sam-
les are naturally filtered (shown by B), and all individuals in the af-
fected samples are naturally filtered (shown by C).

Figure 4: Expected effects of the artificial filtering of outlying compo-
nent trait data with increasing thresholds on the change of sexual se-
lection estimates (compared with the nonfiltered state) in the filtered 
subsamples, when assuming three different scenarios: when there is 
signal filtering by receivers and their filtering threshold is mildly var-
iable (solid line), when degradation increases incoherence between 
mate choice and our measurements (dotted line), and when there is 
neither degradation nor filtering (dashed line). Note the position of 
zero on the y-axis. The capital letters indicate stages where the propor-
tion of individuals subjected to natural filtering still increases steeply 
with the threshold (shown by A), most individuals in the affected sam-
les are naturally filtered (shown by B), and all individuals in the af-
fected samples are naturally filtered (shown by C).

early part of the curve (marked with A in fig. 4), we are well 
below the predominant filtering threshold of receivers, so 
the sample we filter consists largely of individuals that are 
not subjected to filtering by the receivers. Although it cer-
tainly contains all of the individuals that are subjected to 
filtering by the receivers, the number of these is likely low 
compared with the sample we artificially filter. Therefore, 
the change of sexual selection due to the artificial filtering 
will likely be only weakly positive, but it will increase with 
the threshold, mainly because the proportion of the natu-
ronally nonfiltered individuals decreases in the sample. As 
we further increase the artificial filtering threshold (marked 
with B in fig. 4), we approach the natural filtering threshold 
of the population, so the increase of the sexual selection in-
crement becomes less and less pronounced as the last indi-
viduals not subjected to filtering by receivers vanish from 
the sample. Beyond the predominant natural filtering thresh-
hold of the population, we expect only a shallow increase in 
the magnitude of the sexual selection increment. Here, data 
of all individuals in all of the samples we filter are also fil-
tered by the receivers (marked with C in fig. 4). The small 
crease predicted in this section is caused by the increased 
developmental noise and premating degradation. However, component trait 
icoherence may mainly be system-level and not traitwise 
icoherence, and therefore the adaptive response of re-
civers is sexual selection on coherence. Contrary to the 
previous scenarios, artificial filtering is expected to reduce 
sexual selection in the affected sample (dashed line in 
fig. 4). This is because if we remove any component trait 
value, we pull the integrated signal expression estimate 
away from the original value on which natural receivers 
based their mating decisions (i.e., we distort the signal ex-
pression estimate). The combined effect of the distortion 
of all artificially filtered integrated signal expression values 
will be a reduction in the observed strength of the sexual
selection estimate (e.g., the relationship between integrated signal expression and mating success). The decline of estimated sexual selection is expected to become greater when increasing the filtering threshold value because the average discordance between the artificially filtered, and thereby distorted, signal values and the naturally used unfiltered values increases (i.e., an exact inverse of the situation in sec. C of the first scenario above). Again, we cannot predict the exact function shape, and the linear function depicted in figure 4 only serves to illustrate monotonic change. In sum, the curve shapes predicted for the three scenarios are the following: positive values and increasing with a distinct, localized deceleration (filtering); positive values and monotonically increasing with no localized deceleration (degradation); and negative values and decreasing (no filtering, no degradation).

The Study System

Here, we investigate the role of sexual signal coherence in the context of multiple sexual traits in a unique long-term data set of male and female plumage ornamentation from a wild population of collared flycatchers (Ficedula albicollis). Spectral measurements of five plumage areas, some white and some pigmented, indicated that brightness (BRI; across-spectrum reflectance) was correlated across the different areas and this correlation pattern was statistically similar in the two sexes. The same applied to ultraviolet chroma (UVC; relative ultraviolet reflectance). However, few correlations between BRI and UVC traits were significant, indicating that plumage-level BRI and UVC are two separate, integrated signals (Laczi et al. 2011). Moreover, we not only suggested mutual sexual selection for integrated, plumage-level BRI and UVC but also indicated, using a meta-analytic approach, that mutual sexual selection may specifically target plumage-level BRI or UVC expression rather than the separate, correlated component traits of each plumage area (Laczi et al. 2011). Here, we will examine the possible sexual selection role of signal incoherence in BRI or UVC among plumage areas using the analytical approaches outlined above. Our results presented below suggest that signal coherence is not sexually selected in this population but sexual selection depends on coherence. Receivers apparently filter outlying component expression values when assessing the plumage BRI of potential mates.

Material and Methods

Field Methods and Spectral Variables

This study was conducted in our long-term study area of nest box plots situated in the Pilis-Visegrádi Mountains between Szentendre and Pilisszentlászló, Hungary. Data used here were collected in 10 breeding seasons (2009–2018) by capture and spectrometry of parents during nesting development. We obtained research permits from the regional nature conservation authority (KTVF 43355–1/2008, KTVF 509–4/2012, PE/KTF/11978–5/2015, PE/KTF/11978–10/2015, PE-06/KTF/920–7/2018) and ethical permits from the institutional animal welfare committee of Eötvös Loránd University (T-012/2015, T-020/2017). All procedures were performed in accordance with relevant guidelines and regulations.

Because of the low percentage of yearling males and their partly different plumage reflectance from adults (sub-adult plumage), only adult males and their mates were included in the present analyses (835 breeding pairs with complete spectral information from both sexes, a total of 16,700 BRI or UVC entries). Repeated data of the same individuals were retained because the unit of the analysis is the pairing event. Repeated breeding by the same pair in the same year never occurs, and reflectance of an individual changes greatly (Hegyi et al. 2019), so repeated occurrence of the same individual in the data set represents distinct pairing (mate choice) events. Spectral measurements were taken from the forehead, crown, wing patch, wing coverts, and breast. These areas were initially chosen for spectrometry, as they represent two well-known white ornaments, the wing and forehead patch, and the three largest well-defined, more or less homogeneous plumage areas of the species, the dark wing surface and head and the white breast. We used a USB2000 spectrometer, DH-2000 deuterium-halogen light source, R400–7 fiber-optic detector, and the OOIBase software (all from Ocean Optics Europe). Reflectance data were calculated relative to a WS-1–SS white standard (Ocean Optics Europe) and a dark standard (excluding incoming light to the sensor) that were regularly remeasured during the spectrometry sessions. Each plumage area was measured twice. For each plumage area, we calculated BRI (average reflectance from 320 to 700 nm) and UVC (reflectance from 320 to 400 nm divided by BRI) and averaged the values from the two measurements. We restricted our analyses to BRI and UVC, as these represent the main axes of spectral variation (Laczi et al. 2011). We thereby had 20 spectral traits, 10 for each sex (BRI and UVC from each of the five plumage areas). All spectral traits were first standardized for year to correct for among-year variation and to bring their original, sometimes drastically different expression (e.g., dark brown vs. white) to a common, comparable scale. Therefore, all trait expression data used in the following were given relative to the yearly population mean of the given trait, and their unit was standard deviation. We used first principal components (PCs) calculated from year-standardized spectral trait data separately for males and females to estimate the overall signal expression of the...
individual (BPC for BRI with a mean component loading of 0.51 and UPC for UVC with a mean loading of 0.99; see detailed loadings in table S1). The correlation structures of BRI and UVC traits and therefore the eigenvectors of BPC and UPC are very similar across our study years (matrix equality is the best model when running common PC analyses on yearly correlation matrices in the program CPC; Phillips and Arnold 1999; details not shown). We finally note that using models of avian vision to qualify reflectance variation (Delhey et al. 2015) was avoided in our study because the focus was precisely on a putative perceptual mechanism that allows receivers to integrate and compare visual inputs arriving from plumage areas of drastically different reflectance properties. Indeed, we conducted all analyses after converting reflectance variables to a common, standardized scale. Data have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.xwdbrv1fr; Hegyi et al. 2022).

**Statistical Analyses**

Our analyses are based on assortative mating as a sexual selection measure. Assortative mating is the correlation between pair mates in the sexual trait examined. In the relevant literature, it has repeatedly been assumed that positive assortative mating on continuous ornamental characters may arise from mutual sexual selection on these characters, and such studies mostly reported weak or moderate positive correlations (many such studies are reviewed in Jiang et al. 2013). Moreover, recent developments have greatly clarified the conditions in which we can consider assortative mating an index of sexual selection and not an artifact (Class et al. 2017; Indykiewicz et al. 2017). Two alternative, continuous measures of sexual selection could be available in our study system. The first is the mating latency of courting males, which does confirm that reflectance is sexually selected in our population (Hegyi et al. 2019), but it provides a magnitude smaller data set because of its methodological limitations and is therefore unsuitable for our present purposes. The second is breeding date, which because of its multifactorial background, generally gives extremely weak effect sizes (see, e.g., Hegyi et al. 2006 for a large-sample example). Again, it is therefore not suitable for the present study because the artificial removal of outlying component trait data that we perform here is unlikely to meaningfully alter the position of the respective individual in a relationship when overall fit is very low. Here, we therefore use assortative mating to estimate mutual sexual selection but carefully verify the approach for our system as described in “Supplementary Methods” in the supplemental PDF.

When estimating sexual selection on coherence, we first calculated an individual-specific coherence measure for BRI and UVC as the standard deviation of areaspecific BRI or UVC values. We then tested assortative mating correlations between the male and female coherence values of each pair. We ran this analysis using both year-standardized and nonstandardized component trait values.

In the artificial signal filtering (see details in the introduction), we applied assortative mating as a sexual selection estimate. We set a threshold range of 2.0–3.0 SD (with 0.1 SD increments) for BRI and 2.0–2.5 SD (with 0.05 SD increments) for UVC (because of the greater dispersion of the latter trait). Applying a higher resolution (0.05 SD) is possible for BRI, but it leads to the same conclusions. Importantly, we did not detect more than one outlying value for a given individual with any of the thresholds. We illustrate our filtering approach with real data in figure 5. We first calculated assortative mating for each subset of the data (breeding pairs) “detected” by a given male and female threshold combination. As the analysis was conducted at the pair level, we looked for all pairs affected by filtering with the given threshold combination (e.g., 2.0 SD male, 2.5 SD female), so we included a data point in the subset if either member of the pair (male, female, or both) showed an appropriately strong outlying trait value. Our protocol involved (1) the calculation of prefiltering assortative mating correlations based on the nonfiltered original PC data, (2) the replacement of the outlying component value with the population mean (i.e., zero) for each of the affected individuals, (3) the recalculation of the PC analysis for the whole population using the filtered data of the affected individuals, and (4) the recalculation of the assortative mating correlation for the given subset using the new PC data. Substituting the mean of the remaining data instead of the population mean produces practically identical PC scores for the affected individuals (the mean correlation is $r = 0.993$ for the most stringent threshold of 2.0 SD). We thereby obtained $11 \times 11 = 121$ pairs of prefiltering and postfiltering assortative mating correlations for both BRI and UVC.

An alternative approach could have been to use the whole-sample assortative mating pattern as a reference for all subsets (a single prefiltering estimate) and recalculate the assortative mating in the whole sample of 835 pairs after filtering each subset. We present the results of this approach in figure S1 and table S2. This calculation is burdened by two confounding factors that make the results difficult to interpret. First, the proportion of the whole sample represented by the filtered subsets decreases with the thresholds, so the power to detect the filtering effects diminishes along the threshold axes. Second, if outliers systematically distort the integrated signal value of the affected
individuals (because of the distributional properties of the outliers), then the trait values of the subsets will shift because of the filtering, and the whole-sample assortative mating estimate may be strongly distorted. Both of these effects can be seen when comparing the whole-sample results with the subset-restricted results, so we chose to present the latter in the main text.

Finally, we conducted analyses (for BRI and UVC separately) in which threshold-combination-specific prefiltering assortative mating estimates and their changes due to the filtering constituted the individual data points (121 data points in each analysis). In this analysis, we used polynomial regression to examine the effect of the threshold criteria (male and female) on original assortative mating and change in assortative mating. We used polynomial regression and did not fit predesigned functions (asymptotic, linear, etc.), as our analysis was necessarily exploratory for two reasons. First, the function shapes predicted by our verbal model were uncertain, as we outlined in the introduction. Second, unexpected function shapes could have arisen because of the joint action of multiple mechanisms and the contribution of possible factors not included in our model. Threshold values were centered before this analysis to ensure the independence of linear and polynomial terms (Schielzeth 2010). After model simplification with re-introduction, the functions defined by the final models were

Figure 5: Illustration of the artificial filtering procedure with real data from brightness (BRI) values of two males from 2010. In a, the BRI values of the two individuals are shown for each plumage area (circles, W38171; squares, W103654). In b, the individual-level filtering procedure is shown with a threshold of 2.0 SD. Importantly, the dashed lines in a show the mean ± SD of the trait distribution at the population level, which is strictly the same for all traits because of the standardization. In b, on the other hand, the black lines in the middle of the distributions show the individual-specific means calculated from the standardized data of plumage areas. These means are different for each individual and determine the individual-specific placement of the filtering thresholds (mean ± 2 SD; red lines above and below the individual-specific means). Data falling outside the thresholds in either direction are filtered. No filtering takes place in individual W38121. In individual W103654, wing patch BRI deviates from the individual-specific mean BRI by more than 2 SD, and it is therefore removed and substituted by the population mean (zero; see red markings). If we increase the threshold to a more permissive value of 2.5 SD, data of both individuals remain unfiltered. pa = patch; cov = coverts.
compared with our predictions for the three scenarios outlined in the introduction (fig. 4): positive values and increasing with a well-defined deceleration at intermediate parameter values (filtering), positive values and monotonically increasing with no distinct deceleration at intermediate parameter values (degradation), and negative values and decreasing (no filtering, no degradation). All analyses were performed in Statistica version 5.5 (StatSoft, Tulsa, OK).

Results

Assortative mating for individual-level signal coherence, as a measure of mutual sexual selection on coherence, was very low and not significant for either BRI or UVC (Pearson $r < 0.04$).

We analyzed the outcomes of the artificial filtering exercise by looking for the statistically supported patterns of original (prefiltering) assortative mating and change in assortative mating. These are shown in figures 6 and 7, respectively. For results of the polynomial regressions, see table 2.

Original, prefiltering assortative mating was always positive (fig. 6). Original assortative mating in BRI showed significant first- and second-order effects of threshold values in both sexes, and there was also a third-order effect of the female threshold (table 2). Moreover, the second- and third-order effects of the female threshold changed with the male threshold (male × female and male × female$^2$ interactions), and the second-order effect of the male threshold changed with the female threshold (male$^2$ × female interaction). When looking at the supported function (fig. 6a), original assortative mating for BRI showed little change over most of the parameter range, but there was a sharp increase at jointly high values of both thresholds.

When looking at original assortative mating for UVC, we found first-, second-, and third-order effects of the male threshold and first- and second-order effects of the female threshold, and there was an interaction between the first-order effects (table 2). The supported function decreased in the range of low-parameter values and became largely flat when reaching high-parameter values (fig. 6b).

Change in assortative mating in response to the artificial filtering (prefiltered minus original) was nearly always positive for both BRI and UVC (orange areas in fig. 7), although a small decrease appeared when filtering UVC traits with very low male threshold values (blue area in fig. 7b). The pattern of change in assortative mating for BRI (fig. 7a) reflected the first- to third-order effects of male and female thresholds, the interactions of the first-order effects, and an effect of the male threshold on the second-order effect of the female threshold (male × female$^2$ interaction; table 2). In females, change in assortative mating for BRI increased and then broke off with the threshold, although this pattern was more pronounced at high male threshold values. In males, there was an increase, then a decreasing section, followed by another increase at very high threshold values. Finally, change in assortative mating for UVC showed an apparently simple, monotonically increasing pattern (fig. 7b), although the supported function consisted of the first- to third-order (male) and first- to second-order (female) effects of thresholds and two weakly significant interactions (table 2).
As mentioned above for BRI, there was a point at intermediate parameter values of both sexes where the increment of our sexual selection estimate no longer increased and actually showed a decreasing section. A distinct, localized deceleration in the trajectory of the sexual selection increment at intermediate parameter values was an exclusive prediction of signal filtering by receivers (solid line in fig. 4), so these results suggested that male and female BRI traits are subject to filtering in our population. Therefore, we attempted to illustrate the practical importance of filtering for experimental signal manipulations with a simulation using the BRI data. In other words, we aimed to see the magnitude to which filtering by receivers would disturb the interpretation of experimental manipulations of individual component traits in our population. For each component BRI trait of each male in the sample in turn, we changed the expression of the trait to a value close to the limits of the natural distribution. We set the manipulated value to either 5% (BRI reduction) or 95% (BRI increase), where 0% and 100% are the lower and upper bounds of the natural distribution, respectively (a total of 8,350 simulated trait manipulations, 10 for each male). We then calculated the distance of the manipulated value from the individual-specific mean of standardized component BRI values and noted whether the distance exceeded the approximate natural filtering threshold for males in the population (2.3 SD; see fig. 7a). The results of this simulation are summarized in figure 8. For each trait, there was a direction (increase or reduction) in which at least half (but sometimes all) of the manipulated values exceeded the filtering threshold. These values are expected to be ignored by females.

Discussion

Here, we aimed to approach functional signal integration from the perspective of signal processing by receivers. This topic has repeatedly been highlighted but only rarely studied (Miller and Bee 2012; Halfwerk et al. 2019; Mitoyen et al. 2019). We introduced the concept of signal coherence and distinguished two main types of incoherence and the signal processing strategies they are likely associated with. We then used a long-term field data set of male and female plumage reflectance to assess variation in signal coherence and its possible roles in signal processing. Our main goals were to see (1) whether the coherence of reflectance across the plumage was sexually selected and (2) whether coherence acted as a determinant of sexual selection on overall plumage reflectance. The two main approaches we used were accordingly (1) the direct assessment of sexual selection on coherence and (2) the detailed study of how our measure of sexual selection on integrated reflectance (assortative mating) responded to the threshold-based, artificial filtering of outlying component trait data.

Interpretation of the Results

The results illustrate why we were obliged to look at the changes of assortative mating due to the artificial filtering and not the final assortative mating values. Patterns of postfiltering assortative mating would have been greatly confounded by those of prefiltering assortative mating, thereby obscuring the effects of the exercise. Indeed, the prefiltering patterns of assortative mating are at least partly
concave (i.e., nonlinear in a way that blurs the definitive function shape predicted for the case of filtering). But prefiltering patterns of assortative mating are not simply noise that needs to be corrected for. They themselves reveal some characteristics of phenotypic variation in the samples of individuals with outlying component trait values. When looking at BRI (fig. 6a), there is little variation in prefiltering assortative mating except for the upper ends of the threshold scales. The sharp increase observed at high threshold values likely originated from the increased dispersion of BRI in the “affected” samples (i.e., the increased average distance of points from the population mean). This increased dispersion makes our conclusions conservative; see figure S2 and table S3 for details. The prefiltering assortative

### Table 2: Polynomial regressions of original assortative mating and change in assortative mating in relation to centered male and female trait-filtering thresholds (“male” and “female”)

|                | BRI original | BRI change | UVC original | UVC change |
|----------------|--------------|------------|--------------|------------|
|                | F            | df         | F            | df         | F           | df         | F            | df         |
| Male           | 19.43***     | 1, 112     | 14.17***     | 1, 112     | 5.40*       | 1, 113     | 176.92***    | 1, 115     |
| Female         | 74.52***     | 1, 112     | 22.94***     | 1, 112     | 80.20***    | 1, 113     | 116.36***    | 1, 115     |
| Male\(^2\)     | 51.02***     | 1, 112     | 23.01***     | 1, 112     | 136.99***   | 1, 113     | 19.02***     | 1, 115     |
| Female\(^2\)   | 17.16**      | 1, 112     | 71.50***     | 1, 112     | 24.78***    | 1, 113     | 64.36***     | 1, 115     |
| Male\(^3\)     | 2.84         | 1, 111     | 83.82***     | 1, 112     | 4.34*       | 1, 113     | 2.01         | 1, 114     |
| Female\(^3\)   | 144.80***    | 1, 112     | 8.17*        | 1, 112     | .91         | 1, 112     | .07          | 1, 114     |
| Male × female  | 1.03         | 1, 111     | 10.13***     | 1, 112     | 5.94*       | 1, 113     | 13.69***     | 1, 115     |
| Male × female\(^2\) | 5.77         | 1, 112     | 13.77***     | 1, 112     | .05         | 1, 112     | 2.81         | 1, 114     |
| Male × female\(^3\) | 32.67***     | 1, 112     | 1.11         | 1, 111     | .25         | 1, 111     | .13          | 1, 113     |
| Male\(^2\) × female  | 11.93***     | 1, 112     | .02          | 1, 111     | 5.05*       | 1, 113     | .08          | 1, 114     |
| Male\(^2\) × female\(^2\) | .41          | 1, 111     | 1.39         | 1, 111     | .03         | 1, 112     | .01          | 1, 114     |
| Male\(^2\) × female\(^3\) | .54          | 1, 111     | .00          | 1, 111     | .06         | 1, 111     | .02          | 1, 113     |
| Male\(^3\) × female  | 1.98         | 1, 110     | 1.32         | 1, 111     | .46         | 1, 112     | .00          | 1, 113     |
| Male\(^3\) × female\(^2\) | .01          | 1, 110     | .10          | 1, 111     | .14         | 1, 112     | 2.73         | 1, 113     |
| Male\(^3\) × female\(^3\) | .70          | 1, 110     | .01          | 1, 111     | .03         | 1, 111     | .08          | 1, 112     |

Note: Superscript numbers 2 and 3 refer to second- and third-order polynomials, respectively. We applied backward stepwise removal of nonsignificant terms, and the results presented for these reflect their reintroduction to the final model one by one. BRI = brightness; UVC = ultraviolet chroma.

* P < .05.
** P < .01.
*** P < .001.

Figure 8: Percentage of males (out of 835) in which manipulating the brightness (BRI) of a given plumage area to 95% (BRI increase, gray bars) or 5% (BRI reduction, black bars) of the natural range of year-standardized values produces a value that falls outside the approximate natural filtering threshold for male BRI (2.3 SD).
mating function in UVC, on the other hand (fig. 6b), shows a decrease with the thresholds, which supports the scenario of postmating degradation. The proportion of degraded individuals in the sample is expected to increase with threshold values (more extreme data are more likely to be degraded), thereby reducing the strength of the prefiltering mating pattern.

As mentioned above, the definitive results of the filtering exercise can be seen in the changes of assortative mating in response to the artificial filtering. Sexually selected coherence would predict a decline of assortative mating after the artificial filtering. Given that we observed the opposite (i.e., an almost uniform increase; orange areas dominate in fig. 7), sexually selected coherence is not supported. There was also no observable assortative mating for coherence, which again does not agree with sexual selection on coherence. Considering the other two hypothetical scenarios, the increase of the assortative mating increment broke off at intermediate values of artificial male and female filtering thresholds for BRI, which supports signal filtering for the BRI of both males and females. It is very interesting and intuitive that although we do not directly test this here, the suspected natural filtering threshold (where the break occurred) seems lower in males. This is the more conspicuous and more variable sex (Laczi et al. 2011), where two BRI values separated by the same distance on the standardized scale may be easier to discern than in females, thereby possibly causing a lower filtering threshold. There was an unexpected sharp increase in the assortative mating increment at very high values of the artificial male threshold. As in prefiltering assortative mating (see above), this pattern may reflect the increasing dispersion of male BRI with the artificial filtering threshold.

For UVC, the assortative mating increment increased monotonically with artificial male and female filtering thresholds. The function was accelerating with the female threshold and mildly decelerating with the male threshold, and there was clearly no localized intermediate shift in the behavior of the function, as expected in the case of filtering. This monotonically increasing pattern suggests that the assortative mating increment due to the artificial filtering of UVC is caused by the differential degradation of signal components. This is consistent with the decreasing pattern of prefiltering assortative mating and also agrees with our previous finding that UVC (but not BRI) degrades differentially (more strongly in some plumage areas than in others) between the beginning of breeding and the parental care period in this population (Hegyi et al. 2019).

**Potential Pitfalls**

An important immediate question is whether postmating degradation may have destroyed the effect of otherwise present signal filtering on the results for UVC. In other words, can degradation and filtering coexist in the same system, thereby making filtering difficult to detect? We suggest that this may occur only in special systems where the component traits are produced “on the spot” or shortly before mate choice but are then retained and prone to strong degradation before the time of capture and measurement. In collared flycatchers, however, the “last” components of the integrated signal are grown in winter, several months before the courtship period, so much more serious degradation of UVC can be expected before than after mate choice, and therefore filtering by receivers would be unfeasible, given that in a typical individual more than one component ornament would already be degraded by the time of courtship (Hegyi et al. 2019).

A second, equally important question is whether filtering and degradation can reliably be distinguished according to the artificial filtering we recommended here. We suggest two major sources of uncertainty. The most profound one is sufficient sample size. Signal filtering by receivers is likely to evolve with high threshold values so that only a small percentage of the signalers get filtered. Although we had a relatively large sample, the apparent natural filtering threshold for BRI in females (the less distinguishable sex) nevertheless fell to the upper region of our feasible filtering threshold range. With lower sample sizes, the upper end of the threshold range would be even lower, and we would therefore conclude that degradation, but not filtering, occurs for female BRI. It is therefore imperative to ensure that the threshold range of the artificial filtering sufficiently covers the natural distribution range of outliers in the population.

The second possible cause of uncertainty is the relative importance of the two drivers of the function characteristic to filtering (first scenario, solid line in fig. 4). In the first part of the curve (A and B), the increase of the assortative mating increment is due to (1) the proportion of our sample that is naturally filtered and (2) the magnitude of the effect size distortion caused by the inclusion of the outlier. After reaching the natural filtering threshold, only driver 2 remains. If driver 2 is more important than driver 1, it may become difficult to detect the local decrease of slope that is characteristic of the suggested curve of natural signal filtering. However, we anticipate that the percentage of the affected data (driver 1) will generally be more important than the mean magnitude of the distortion caused by a single point (driver 2). The results support this view. At the presumed natural threshold, the sudden decrease of slope is very drastic in both males and females. We recommend the analyses of other natural data sets and Monte Carlo simulations to test this point of uncertainty.

Another concern regarding our results is that if there is a correlation between trait mean and variance, individuals
with higher overall BRI expression may more easily get filtered by receivers, or in other words, filtering may exert selection against bright individuals. We therefore analyzed for each filtering threshold value the relationship between BPC and the probability to get filtered in our filtering exercise. The relationships were weak for male BRI but significantly positive for female BRI. However, any observed positive mean-variance correlation was apparently caused by the outlying values, as there were nonsignificant or even negative relationships between filtered BPC values and the probability of filtering in both sexes (see detailed results in table S4). It therefore seems that in our study system, filtering does not select for low BRI when discounting the distortion caused by outlying values.

A final concern regarding the analysis might be that the greater the natural filtering threshold, the more difficult it becomes to distinguish the results from a scenario where receivers filter each component trait based on their own distributions (i.e., absolute, not relative, extremes). This simply reminds us to apply the analysis only in the right system. Trait-based absolute filtering is expected to appear only in correlated multitrait systems where the signal traits function separately. Component signal filtering as we mean here can be interpreted and expected only in systems where the signal component traits are functionally integrated and work as a single trait (such as our study system; Laczi et al. 2011).

**Implications for Sexual Selection Research**

Our results for BRI suggest that receivers filter multiple redundant sexual traits in our population. How important is this finding? Correcting for filtering substantially increased the observed strength of our sexual selection estimate. The increase was around 50% at the combination of the apparent filtering thresholds for males (2.3 SD) and females (2.7 SD; original value: ~0.3; increase: ~0.15; compare figs. 6a and 7a). However, filtering will not measurably affect sexual selection on the integrated trait at the population level because of the low number of the individuals subjected to filtering. Two principal implications of signal filtering concern the empirical study of multiple-ornament systems and the evolution of conspicuous traits and preferences.

Signal filtering may have the greatest practical relevance to experimental studies of sexual signals. The advantage of exaggerated component trait expression in an integrated signal complex (Delcourt et al. 2012) will be partly counteracted by signal filtering because the exaggerated value will be disregarded by the receiver if incongruent with the expression of other components. Threshold-based filtering thereby definitively hampers experimental studies of individual trait function and suggests that existing studies on the subject need to be reevaluated in systems with consistently correlated traits (i.e., most systems; see table 1). Manipulated sexual traits are typically designed to reach the extremes of the natural expression range and will often deviate from other correlated traits and thereby elicit little or no response from receivers if signal filtering operates. In figure 8 we present an example estimate of this problem using our own data. The example shows that manipulations of individual BRI component traits of males toward their natural extremes are very likely (in some traits and directions, certain) to produce trait expression values that are deviant from the rest of the phenotype and will therefore likely be filtered and not considered by females. The result of such experimental manipulations will therefore probably be a lack of response by the receivers and a conclusion that the given aspect of coloration is not sexually selected.

It is impossible to assess the influence of signal filtering on previously conducted single-trait manipulations based on the literature, as it is certain that many studies with nonsignificant results remain unpublished and many correlated “sister traits” (i.e., potential integrated trait components) remain unknown. However, the perspective of sexual trait correlation structure may bring us closer to explaining results of the few mate choice experiments that manipulated two or more sexual traits incoherently (see also Smith and Evans 2013). For example, signal filtering may underlie preference switches caused by an asymmetrical mimic (a third stimulus similar to one of the original stimuli; Royle et al. 2008; Griggio et al. 2016), while sexual selection on signal integration may lead to stabilizing sexual selection on components of a correlated multicomponent signal when these components are manipulated incoherently (Brooks et al. 2005; Tanner et al. 2017).

For future experimental studies of the functioning of correlated ornamental traits, we suggest the parallel manipulations of all putative component traits to similar positions of their respective ranges as a first step. The parallel manipulation could possibly target multiple different expression levels. If this experiment produces the expected response by the receivers, we can conclude that an integrated signal is operating. If there is no response or unexpected (e.g., nonlinear) response by the receivers even though relative measures suggested directional sexual selection, we may continue by manipulating the correlated traits one by one. If even this does not yield a clear result (e.g., a suggestion that one of the traits is the true signal), then two phenomena may explain the results. First, that the true signal is outside of the set of traits we assessed, but it correlates with these traits. Second, that we missed one or more component trait(s) and even our parallel manipulations produced an incoherent phenotype (with the nonmanipulated traits now being the outliers). In sum, manipulation studies of multiple ornaments become very complicated if the ornaments
are correlated, but doing independent manipulations of such traits as a first or only step is clearly undesirable.

From an evolutionary viewpoint, signal filtering may have broad relevance to signal evolution and signal-preference coevolution and may give rise to several questions. Indeed, the mere concept of signal filtering might be criticized, as it may open avenues for “cheating” by signalers. For example, signalers may evolve to produce only the few least expensive components at a high expression level and bring down the more expensive components to filtered expression levels. Furthermore, individuals that have happened to produce a poor component trait may deliberately damage this trait to get it filtered, thereby ensuring a positive overall picture (for a conspicuous example of “selective” signal display, see Gross et al. 2007). These suggestions assume the evolution of sophisticated allocation or manipulation strategies among components of the ornamentation phenotype. We can raise several immediate theoretical arguments against the evolution of such strategies. First, it is far easier to produce “outlyingly” poor-quality component traits relative to a high average expression level than relative to a low average expression level. Therefore, the cheating may only help high-quality individuals to further increase their success but would not help the poorest-quality individuals to hide their poor quality. Second, the evolution of active allocation among correlated components of an integrated signal may disrupt their correlation structure and may lead to evolution of counterstrategies whereby receivers focus on the most expensive and hard-to-cheat components and ignore the rest. Third, such strategies necessitate that signalers are aware of all of their own component trait expression levels relative to the other components and the population average, and this is highly unlikely. For example, a courting collared flycatcher male will never see its own crown or forehead coloration, and it will probably not have the time to look around to assess the coloration of other courting males in the population. Fourth, these strategies would also require that individuals can independently and accurately manipulate all of their ornamentation components, which may not be feasible in most systems owing to developmental and other physical constraints. However, the above discussion indicates that signal filtering, if present, will not only have implications for our studies of mate choice but also seriously affect how we think about the evolution of ornament integration, ornament processing by receivers, and the coevolution of the two. These topics will therefore require further theoretical and empirical treatment. It is important to note here that there has been much study of related phenomena in different systems, including, for example, the honesty and phenotypic links of a single signal (Rohwer and Rohwer 1978; Levin et al. 2018; Taff et al. 2021) and the processing of multiple, independently evaluated, inconsistent signals (Møller et al. 1998; Tibbetts and Izzo 2010; Murray et al. 2018). The findings of these studies may help build the theoretical and empirical framework needed for the fruitful study of coherence in integrated signals.

How does signal filtering fit into existing theory on the evolution of multiple sexual traits? Classical models suggested that preference for multiple indicators of the same aspect of quality cannot persist if the assessment of multiple sexual traits is costly (Iwasa and Pomiankowski 1994). This suggestion is certainly not supported by the prevalence of sexual trait interrelation in nature (table 1), and we see two straightforward solutions to the contradiction in our study system. One solution is that receivers may assess integrated signal expression “at a single glance,” with minimal added costs of “going through” the multiple component traits (Pérez-Rodríguez et al. 2017; Halfwerk et al. 2019), and signal filtering may be a passive consequence of this overall assessment (Miller and Bee 2012). The second solution is that receivers are under selection to detect and counteract reductions in signal reliability (Patricelli et al. 2016). The principal source of such unreliability may be an evolutionary conflict of interest between signaler and receiver concerning reliability (Kokko and Jennions 2014). Modeling suggests that such conflict of interest may lead to preferences for multiple redundant quality indicators even if additional assessment is costly (Van Doorn and Weissing 2006).

Conclusion

Most study systems of sexual selection are characterized by multiple sexual traits (Hebets et al. 2016), and there may be many more such traits in some systems than we are aware of. Fundamental evolutionary and proximate mechanisms (Tomkins et al. 2004; Blas et al. 2006) drive multiple sexual traits toward correlated expression (table 1), and such correlated expression has obvious relevance to the receivers, given the limited reliability of any individual trait (Johnstone and Grafen 1992). Still, although the correlation structure of multiple sexual traits receives more and more attention (Hebets et al. 2016), the implications of this correlation structure for functional integration by sexual selection remain poorly known. Here, we attempted to draw attention to this topic by describing the possible forms of signal incoherence and proposing and testing ways in which incoherence may impinge on sexual selection. Alarmingly, our results indicate signal filtering by receivers in a complex of distinct sexual traits where several component traits of the integrated signal (such as the reflectance of a white wing patch) readily lend themselves as candidates for an independent signal. Consistently correlated multi-component sexual trait systems are likely very frequent in nature (see the introduction). Therefore, signal coherence
assessment by receivers has broad implications for the design and interpretation of empirical work and potentially affects a wide range of trait types and taxa. Accordingly, studying signal coherence and its perception represent an important direction toward the better understanding of systems with multiple sexual traits.

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Statement of Authorship

G.H. conceived the study. All authors collected data in the field. M.L. compiled the data set. G.H. analyzed the data and wrote the first draft. All authors contributed to the final version and approved submission.

Data and Code Availability

Data have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.xwdbrv1fr; Hegyi et al. 2022).

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"This bird is the *Cyanura macrolopha* of naturalists, and the genus it belongs to is distinguished among our jays by the elegant crest that all the species possess, as well as by the rich blue color that shows particularly on the wings and tail, which are also barred with black.” From "The Long-Crested Jay" by Elliott Coues (The American Naturalist, 1871, 5:770–775).